Evolution de la niche climatique et de la distribution géographique des espèces végétales alpines

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Et voilà, c'est fini. Une histoire entamée il y a quelques années déjà et qui s'achève avec une légère tristesse. Ma soutenance a déjà eu lieu au moment où j'écris ces remerciements, et au lieu de l'exercice académique auquel je m'attendais, elle a été un réel moment de plaisir. Cette mâtinée a été l'occasion de partager le fruit du travail de ma thèse avec vous tous, dans une ambiance très chaleureuse : un point final qui reflète bien ces belles années passées au LECA.

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Ah, les copains du bureau... 205 ou 206, c'est ça? Vous m'avez accompagné au jour le jour pendant trois ans et c'est largement grâce à vous si j'ai passé une thèse aussi agréable. Malgré le manque d'espace, le bureau encombré de diverses saloperies, la grande fissure du mur du fond, on s'est bien marrés et je vous avoue avoir un peu peur de ne jamais retrouver cette ambiance là plus tard. J'emporterai avec moi quelques souvenirs: de gros fou-rires, des cafés, des cafés, et encore des cafés, quelques bières parfois, mais seulement après 16h, des petits verres de la vulnéraire du 'Père Michel', d'accord là c'était plutôt vers 11h mais il faisait froid quand même, des vidéos de la finale du championnat du monde de 'dancehall queen', nos petites sessions musique avec Ju le matin avant que le bureau ne se remplisse, des cafés, le casque de Loïc bien vissé sur ses oreilles, nos longues discussions PD/conservation en bas du labo avec LaureZ, les aventures de 'la bagnole à Damien', des cafés, des scripts R échangés (avec souvent un ‘eval(parse(paste(‘ dedans), des chansons pourries que l'un d'entre nous mettait dans la tête des autres pour toute la journée, encore des cafés... et j'en oublie. LaureZ, Ju, Dam et Loïc, merci à vous quatre pour tous ces moments partagés au labo comme en dehors, j'espère que vous prendrez bien soin du petit Brad et que vous me garderez un petit coin de bureau (près des piquets à mouton?) pour quand je passerai vous voir. Enfin, merci à toi Charogne (ou Mimine) d'avoir veillé sur nous sans jamais broncher!

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victoire mais sans jamais lever la coupe. C'est un grand regret que nous partageons. Merci à tous les autres joueurs pour tout ces bons moments que nous avons passé sur le terrain: les anciens comme Taraf et Mika, et la nouvelle génération des Johan, captain' Flo, Renaud, Marco, 'super' Marti, Arthur, Tristan et Eymeric, mais aussi nos fidèles supportrices: Cindy et Charline. Pour nous ramener un de ces jours la coupe rappelez vous ces deux conseils: un dribble c'est bien joli mais ça vaut pas un tacle et surtout... revenez en défense bordel!

Merci aussi à vous tous que j'ai croisés au LECA, et qui a travers un café partagé, un bonjour dit avec le sourire, une bribe de discussion à la cafét' à midi, une soirée beaujolais nouveau dans un pub irlandais rempli de skin heads ou une blague dans un couloir ont égayé la vie dans ce labo. L'ambiance au LECA est vraiment excellente (je ne suis pas le seul à le dire) et ça aide à se lever le matin pour venir bosser!

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Enfin, j'arrive à ton cas Laure. Tu es mon double dans tout ce que j'entreprends et nombre des idées qui sont couchées dans ce manuscrit viennent de toi. Quel besoin d'écrire ici tout ce que tu sais déjà? Merci tout simplement de me rendre heureux chaque jour.

AVANT-PROPOS

Ce manuscrit est la synthèse de trois années de travail et présente ma contribution personnelle à certaines problématiques de recherche. Tout ceci a été rendu possible grâce à diverses aides, qu'elles soient financières, scientifiques ou logistiques.

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Enfin, une grande partie de mon travail a été réalisée en étroite collaboration avec la Station Alpine Joseph Fourier (SAJF). Les nombreuses discussions que j'ai eues avec les membres de la SAJF m'ont en effet permis d'apprendre à connaître les plantes alpines et leur biologie, mais aussi de mieux cerner les problématiques de recherche essentielles concernant la flore alpine. L'aide de la SAJF a également été déterminante dans les différentes expériences que j'ai entreprises. Mon manuscrit de thèse ne reflète pas l'étendue de ces collaborations et je tiens à mentionner que deux études sur les traits fonctionnels des plantes alpines menées au col du Lautaret ont été publiées (Albert et al. 2010, Boucher et al. 2013) et que j'ai mis en place en juillet 2011 un jardin commun pour étudier l'adaptation locale chez *Polygonum viviparum*, qui devrait fournir des résultats dans les années à venir.

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LISTE DES PUBLICATIONS

Chapitre 1

Münkemüller, T., **Boucher, F.C.**, Thuiller, W., & Lavergne, S. Common conceptual and methodological pitfalls in the analysis of phylogenetic niche conservatism. En préparation.

Boucher, F.C., Thuiller, W., Davies, T.J. & Lavergne, S. Neutral biogeography and the evolution of climatic niches. En révision à American Naturalist.

Chapitre 2

Boucher, F.C., Renaud, J., Schiffers, K.H., Davies, T.J., Arroyo, M.T.K., Aubriot, X., Evans, M.E.K, Guerrero, P.C., Haevermans, T., Midgley, G.F., Mouillot, D., Ronce, O., Roquet, C., Tonnabel, J., Thuiller, W., & Lavergne, S. Punctuated evolution and moderate phylogenetic niche conservatism across 125 clades of plants and vertebrates. En préparation.

Chapitre 3

Boucher, F.C., Thuiller, W., Roquet, C., Douzet, R., Aubert, S., Alvarez, N. & Lavergne, S. (2012) Reconstructing the origin of high-alpine niches and cushion life form in the genus *Androsace* (Primulaceae). Evolution. 66, 1255–1268

Roquet, C.*, **Boucher, F.C.***, Thuiller, W. & Lavergne, S. (2013) Replicated radiations of the alpine genus *Androsace* (Primulaceae) driven by range expansion and convergent key innovations. Journal of Biogeography. Early online. * les deux auteurs ont contribué également à cet article.

Chapitre 4

Aubert, S., **Boucher, F.C.**, Lavergne, S. & Choler, P. A worldwide catalogue of cushion plants 100 years after Hauri and Schröter. Proche de la soumission.

Boucher, F.C., Lavergne, S., Choler, P. & Aubert, S. The history of the cushion life form in Angiosperms. En préparation.

Annexe

Boucher, F.C., Thuiller, W., Arnoldi, C., Albert, C.H. & Lavergne, S., (2013) Unravelling the architecture of functional variability in wild populations of *Polygonum viviparum* L. Functional Ecology. 27, 382–391

INTRODUCTION

1. Contexte général : l'étude de la biodiversité

La biodiversité est un terme qui englobe la diversité biologique à différents niveaux d'organisation, comme la diversité génétique au sein d'une espèce, la diversité des espèces au sein d'un écosystème, ou même la diversité des écosystèmes sur Terre. Les changements globaux actuels, qui comprennent notamment le changement climatique, les changements d'utilisation des terres et l'augmentation des flux de personnes et de marchandises, ont des conséquences importantes sur la biodiversité (Chapin III et al. 2000, Parmesan 2006). Ces changements ont déjà conduit à l'extinction de nombreuses espèces depuis plusieurs décennies (Diamond & Case 1986) et pourraient en causer beaucoup d'autres (Bellard et al. 2012), engendrant ainsi la sixième grande crise d'extinction qu'a connu la Terre. A un niveau d'organisation plus élevé, les écosystèmes sont également impactés, et leur fonctionnement s'en trouve perturbé (Schroter et al. 2005). Face à cette situation il devient urgent d'étudier la biodiversité, non seulement pour prédire son avenir face aux changements globaux et fournir des éléments de décision à la société (Thuiller 2007), mais également pour comprendre les mécanismes responsables de ses origines, de son évolution et de son maintien.

Comprendre les déterminants de la distribution spatiale de la biodiversité fait partie des questions importantes à aborder. La biogéographie est la science qui s'intéresse à la distribution des espèces et écosystèmes. Même si cette discipline est relativement jeune, elle a déjà accumulée de nombreuses connaissances et intégré de nombreux concepts et techniques venues d'autres branches de la biologie, comme l'écologie des communautés ou la macroévolution. Cependant, des questions comme « Pourquoi y a-t-il plus d'espèces dans telle région que dans telle autre? » ou « Qu'est-ce qui limite la distribution de cette espèce ? », restent encore largement à explorer.

Ma thèse s'inscrit dans cet objectif général de compréhension de la distribution spatiale de la biodiversité.

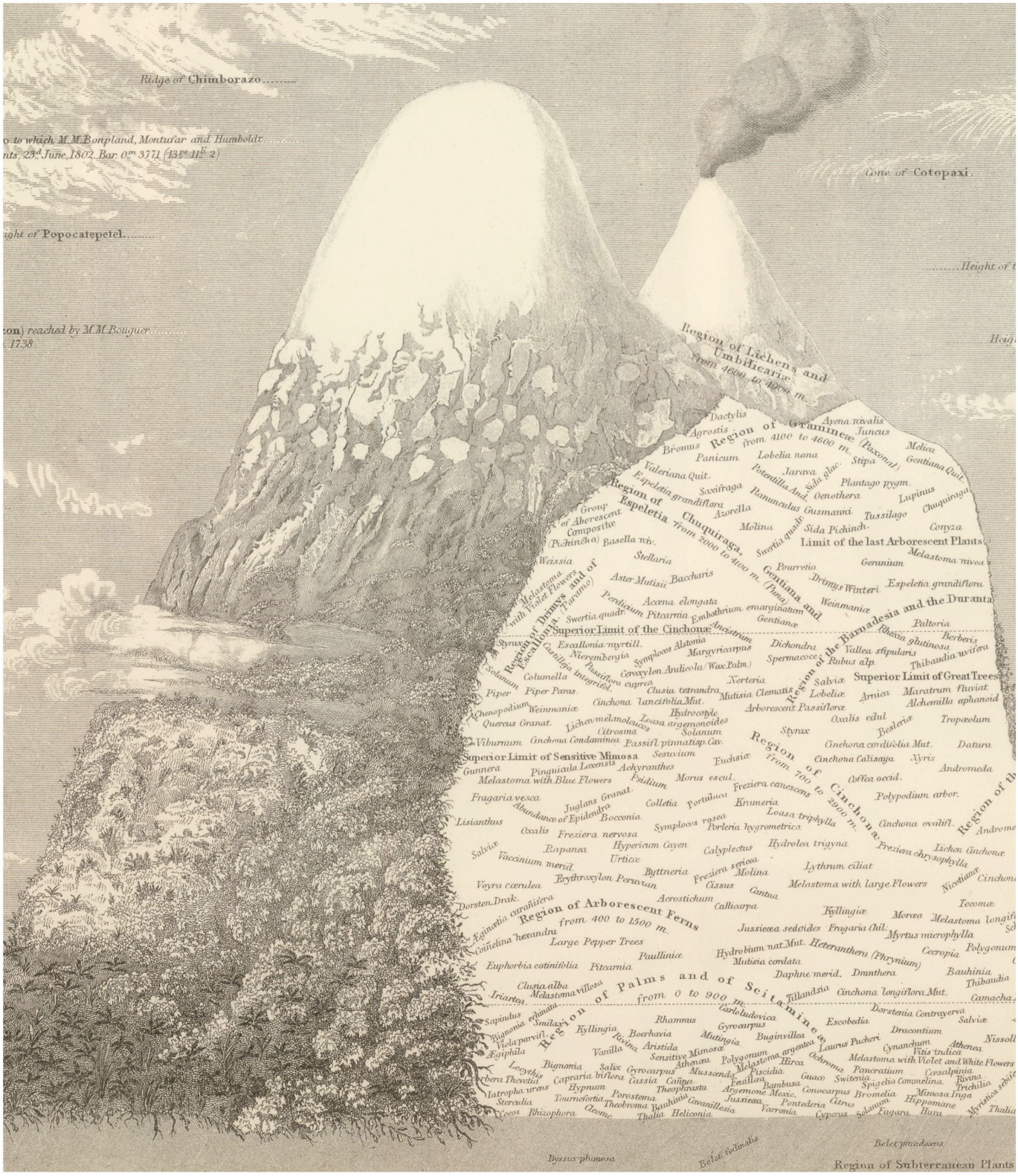

Figure 1. Premier pas de la biogéographie. Ce dessin d'Alexandre von Humboldt datant de 1805 décrit la distribution des plantes du pied au sommet du volcan Chimborazo (Equateur). Von Humboldt y distingue différent étages de la végétation et montre que leur richesse diffère: si le pied du volcan est la zone la plus riche, une zone d'altitude intermédiaire qui correspond à la limite supérieure de la forêt héberge également de nombreuses espèces. Le nuage dessiné au niveau de la zone intermédiaire suggère que l'humidité est la cause de la richesse de la zone intermédiaire. On notera la présence de plantes en coussins du genre *Azorella* (entre autres).

2. La biogéographie depuis les pionniers jusqu'aux concepts modernes

2.1. Décrire la distribution des espèces

Les limites de distribution des espèces ont été observées et leurs causes ont commencé à être recherchées depuis longtemps (Pline 79-77 avant JC). Cependant, cela fait seulement deux siècles qu'Alexandre von Humboldt (1805), Augustin de Candolle (1820), puis Alfred Wallace (1860) ont permis d'en envisager la réponse en jetant les bases de la biogéographie. Au cours de voyages d'exploration dans diverses régions du monde, ils ont dans un premier temps décrit la distribution des espèces (Figure 1). Leurs nombreuses observations détaillées ont permis de décrire les principaux patrons biogéographiques. Ainsi, de Candolle remarquait déjà en 1820 que des habitats pourtant similaires étaient occupés par des espèces de plantes différentes en Amérique du Nord et en Europe. Ceci l'a conduit à distinguer les 'stations' (type d'habitats favorables) et les 'habitations' des plantes (lieux géographiques où elles se trouvent), et donc à supposer que des barrières géographiques limitent la distribution des espèces. Wallace (1860) a lui aussi suggéré la présence de barrières géographiques, comme la ligne qui porte son nom et sépare les faunes indomalaises et australasiennes. Les barrières géographiques ou les autres formes de limites à la dispersion font aujourd'hui partie des concepts fondamentaux de la biogéographie.

Les premiers biogéographes ont également révélé que les écosystèmes n'ont pas tous la même diversité. Ainsi, von Humboldt (1805) a remarqué que certains étages de la végétation des montagnes tropicales comprenaient plus d'espèces que d'autres (Figure 1). Wallace a quand à lui été le premier à décrire un des patrons les plus marquants de la biogéographie, le gradient latitudinal de diversité (Figure 2) :

'Animal life is, on the whole, far more abundant and more varied within the tropics than in any other part of the globe, and a great number of peculiar groups are found there which never extend into temperate regions'.

A. R. Wallace 1876

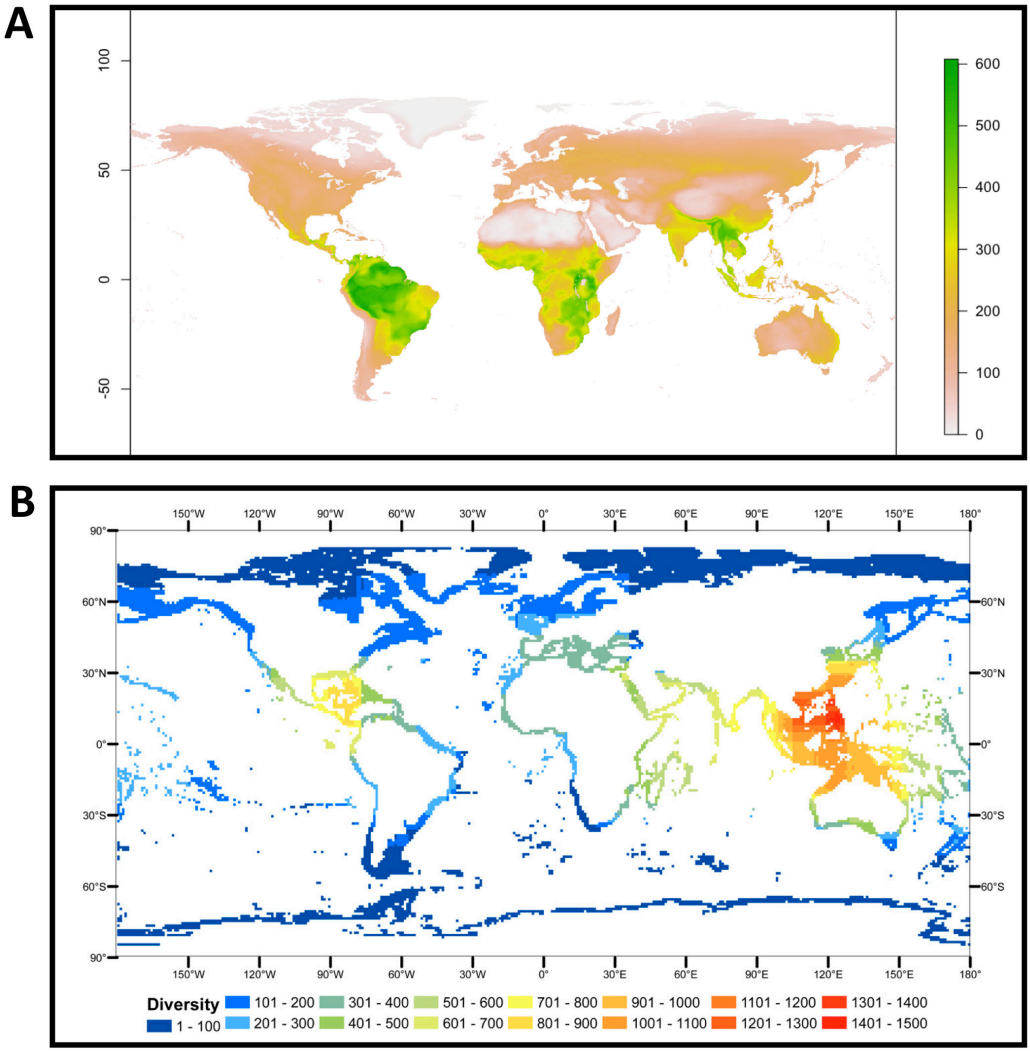

Figure 2. Gradient latitudinal de diversité: observations et explications. Le gradient latitudinal de diversité est le patron le plus clair de la biogéographie. Il a été observé chez la plupart des groupes taxonomiques, comme illustré ci-dessus chez les oiseaux (A, l'échelle de couleur à droite indique le nombre d'espèces par pixel, carte réalisée par Julien Renaud) et les bivalves marins (B, d'après Jablonski et al. 2013). De multiples explications du gradient de diversité ont été proposées, comme la plus grande productivité des milieux tropicaux qui permettrait d'abriter plus d'espèces (Currie et al. 2004), une plus grande stabilité du climat dans le passé sous les tropiques (Brown & Lomolino 1998), l'origine tropicale de nombreux groupes combinée à un faible nombre de transitions vers les climats tempérées (Wiens & Donoghue 2004) ou encore des taux de diversification plus élevés sous les tropiques (Allen & Gillooly 2006), entre autres.

Le gradient latitudinal de diversité a stimulé de nombreux travaux de recherche depuis sa description, mais les développements récents de phylogénies de grands groupes d'organismes (Davies et al. 2004, Bininda-Edmonds et al. 2008, Jetz et al. 2012) et de

larges bases de données sur la distribution des espèces permettent aujourd'hui d'aborder cette question à l'échelle du globe. Cependant, les causes du gradient latitudinal de diversité continuent d'être débattues aujourd'hui (Jablonski et al. 2006, Allen & Gillooly 2006, Dowle et al. 2013, Jansson et al. 2013). Plus généralement, les processus responsables des différences de biodiversité entre régions sont encore mal compris, qu'il s'agisse de différences de richesse spécifique ou de diversité fonctionnelle. En particulier, déterminer l'importance relative de la dispersion, de l'environnement, des interactions biotiques et des processus évolutifs sur la distribution de la biodiversité reste une question des plus importantes en biologie (Hubbell 2001, Ricklefs 2004, Wiens & Donoghue 2004).

2.2. L'influence de l'environnement sur la distribution des espèces : la niche écologique

L'influence de l'environnement, et en particulier du climat, sur la distribution des espèces a été rapidement identifiée. Ainsi, de Candolle (1820) remarquait qu' *'une partie du phénomène de la distribution des végétaux dans les pays divers paraît bien tenir à l'influence appréciable de la température'*.

Cette influence de l'environnement sur la distribution d'une espèce est aujourd'hui caractérisée par sa niche écologique. La niche est définie comme l'ensemble des conditions environnementales permettant à des populations d'une espèce d'avoir un taux de croissance strictement positif (Grinnell 1917). Au cours de ma thèse, je me suis plus particulièrement intéressé à la niche climatique, qui caractérise les conditions climatiques favorables pour l'espèce. La niche climatique ne représente qu'un aspect de la niche écologique d'une espèce, qui comprend également les interactions biotiques avec les autres espèces (compétition, prédation, facilitation ; Hutchinson 1957), Dans la suite de ce manuscrit, et en l'absence de précisions supplémentaires, le terme 'niche' devra être entendu comme 'niche climatique'.

La distinction entre niche fondamentale et niche réalisée est cruciale (Hutchinson 1957, Pulliam 2000, Sobéron 2007). Si la niche fondamentale est définie comme l'ensemble des conditions climatiques permettant à une espèce de se reproduire en l'absence d'interactions biotiques, la niche réalisée comprend également l'effet des interactions

biotiques et des limitations de dispersion (Figure 3). La niche fondamentale est donc déterminée par des traits de réponse au climat (physiologiques, morphologiques, etc.) qui ont généralement une forte base génétique (comme la tolérance à la sécheresse chez le chêne liège, Ramirez-Valiente et al. 2009 ; ou la limite thermique maximale dans le genre *Drosophila*, Kellermann et al. 2012). Mais en pratique, lorsque nous mesurons la niche d'une espèce en croisant des informations sur sa distribution et des données climatiques, nous étudions en fait sa niche réalisée, qui résulte des diverses

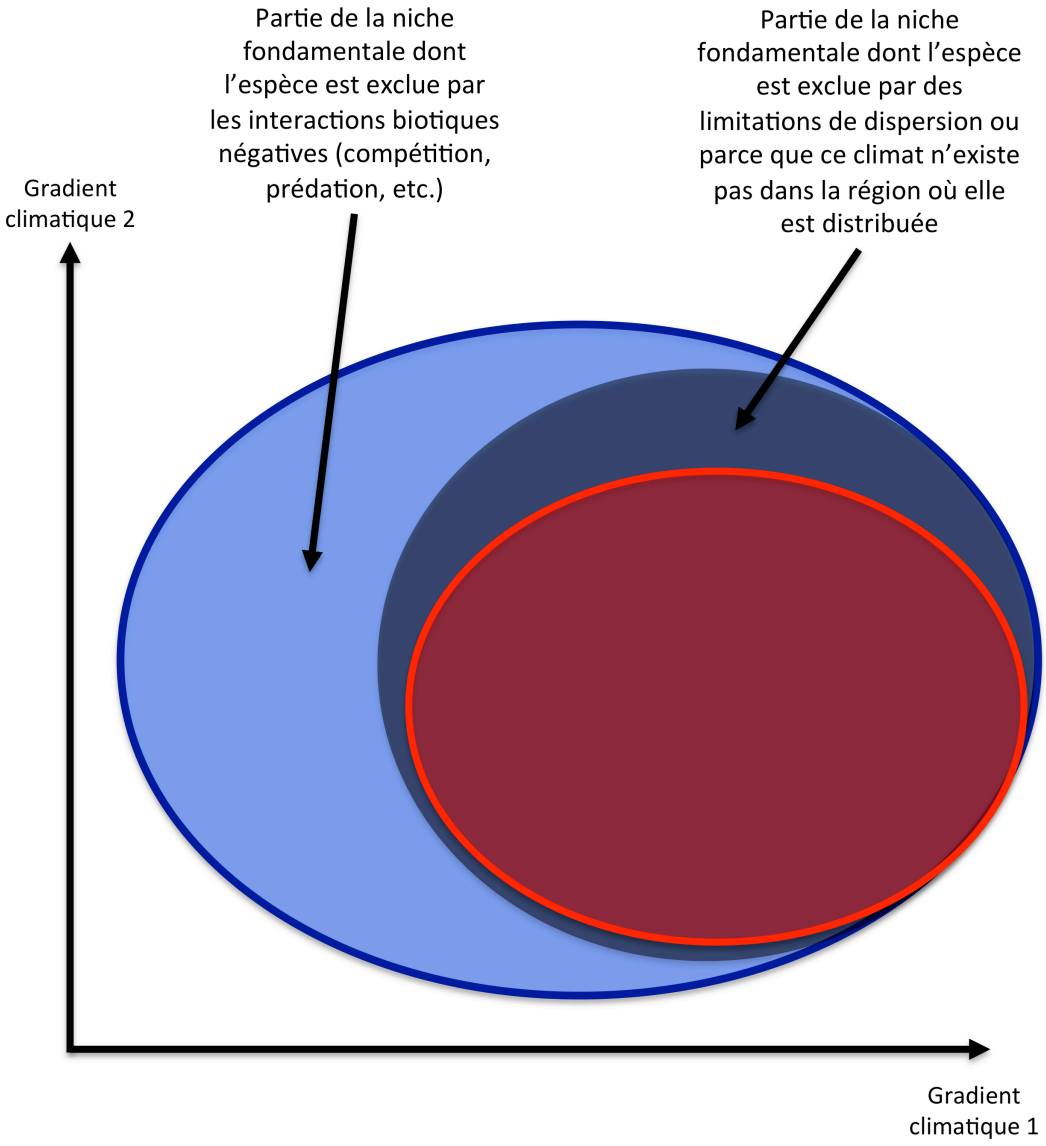

Figure 3. Niche fondamentale et niche réalisée. Ce schéma montre comment la niche climatique fondamentale et la niche climatique réalisée d'une espèce peuvent différer. La niche fondamentale (bordure bleue) traduit les capacités physiologiques de l'espèce à vivre dans une certaine gamme d'environnements (définis ici sur deux gradients climatiques). La niche fondamentale peut être limitée par des interactions négatives et des limitations de dispersion et certains environnements ne sont pas occupés par l'espèce même si sa physiologie le permet. Les influences conjuguées de la niche fondamentale, des interactions biotiques, des limitations de dispersion et de la disponibilité de l'environnement produisent la niche réalisée de l'espèce, c'est-à-dire l'ensemble des environnements qu'elle occupe effectivement (bordure rouge).

composantes que nous avons évoquées. En effet, la niche climatique d'une espèce est souvent estimée au moyen de modèles corrélatifs qui relient des données de présence et d'absence de l'espèce aux conditions climatiques : les modèles de distribution (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Les modèles de distribution ont connu un essor impressionnant depuis une vingtaine d'années et sont notamment utilisés pour projeter les conséquences des changements globaux sur la biodiversité (Thuiller et al. 2011) ou en biologie de la conservation (Araujo et al. 2004, Kujala et al. 2011).

2.3. Evolution de la distribution des espèces

La distribution d'une espèce n'est pas statique : elle est susceptible d'être modifiée puisque la niche peut évoluer, comme toute caractéristique d'une espèce. Cette remarque paraît aujourd'hui anodine mais elle ne l'a pas toujours été, puisque les espèces ont longtemps été regardées comme des entités 'fixées' dans le temps et l'espace (Linné 1735). Ainsi, à l'époque de de Candolle (1820) *'il est encore une partie des faits* [concernant la distribution des espèces] *qui échappe à toutes les théories actuelles, parce qu'elle se lie à l'origine même des êtres organisés'*. La théorie de l'évolution, proposée dans les décennies suivantes (Wallace 1858, Darwin 1859), permettra de comprendre que toutes les espèces ne sont pas apparues au même moment ni au même endroit sur Terre, et que la distribution et les tolérances climatiques des espèces sont susceptibles de changer.

Ces différences dans la date et le lieu d'origine des espèces ainsi que la capacité de leur distribution et de leur niche à évoluer sont au cœur des questions qui sont aujourd'hui posées sur l'origine des gradients de diversité. En effet, la plupart des grands groupes d'organismes sont apparus sous des climats tropicaux qui étaient jadis répandus sur la quasi-totalité du globe (Fine & Ree 2006). Ceci pourrait suffire à expliquer pourquoi les milieux tropicaux sont plus riches, puisqu'ils ont simplement eu plus de temps pour accumuler des espèces (hypothèse du 'Time for Speciation', Fisher 1960). Si les organismes ont eu en plus des difficultés à s'adapter aux climats tempérés, ceci augmenterait encore la pauvreté relative des régions situées aux hautes latitudes (hypothèse du 'Tropical Niche Conservatism', Wiens & Donoghue 2004). Au contraire, si cette adaptation a été facile, d'autres explications du gradient de diversité seraient à

trouver (modèle 'Out of the Tropics', Jablonski et al. 2006), comme par exemple des taux de diversification plus élevés sous les tropiques (Cardillo 1999).

Au cours de ma thèse, je me suis intéressé à deux objectifs principaux. J'ai tout d'abord cherché à déterminer quels sont les processus qui régissent l'évolution de la niche climatique des espèces. Ensuite, j'ai essayé de déterminer les conséquences de l'évolution des niches climatiques sur la distribution spatiale de la biodiversité, en m'intéressant particulièrement aux espèces végétales alpines.

3. L'évolution des niches climatiques : contexte scientifique et enjeux

'A familiar experience when traveling across a continent is to see a widely distributed species decline in abundance until it disappears from the local community. Such range boundaries often coincide with discontinuities in the habitat, for example, with a mountain range or the ocean's edge. But in other cases the boundaries lie at seemingly arbitrary points along continuous gradients of environmental factors such as temperature and moisture. Such boundaries confront us with a mystery: What sets the geographical limits on a species' range? […] But from an evolutionary perspective, there is a deeper mystery. Why do the populations at the range margin not adapt to their local conditions and then spread outward?'

M. Kirkpatrick & N.H. Barton 1997

3.1. Les outils de la macroévolution : modèles statistiques et phylogénies

Pour étudier l'évolution des niches climatiques des espèces, j'ai principalement utilisé des outils et des concepts issus de la macroévolution. La macroévolution est l'étude des phénomènes d'évolution à un niveau plus large que celui de l'espèce, elle englobe la paléontologie (étude des espèces éteintes) et la néontologie (étude du passé des espèces vivant actuellement). C'est une science historique puisqu'elle s'intéresse à des phénomènes tellement longs ou anciens qu'il est impossible de les observer directement ou de les manipuler (les temps de spéciation sont de l'ordre de 100 000 ans chez les vertébrés et les plantes, Avise et al. 1998). L'expérimentation est quand à elle presque inaccessible vu les échelles de temps impliquées, excepté en microbiologie (Lenski & Travisano 1994, Gravel et al. 2011, Le Gac et al. 2012).

Privée d'observation et d'expériences, la macroévolution utilise l'inférence statistique comme outil privilégié, qu'il s'agisse de reconstruire des phylogénies ou d'étudier l'évolution des traits des espèces dans le passé. Si la distinction entre macroévolution et microévolution (l'évolution au sein d'une espèce) peut paraître quelque peu arbitraire et

a été vivement critiquée (Dawkins 1996, revue dans Shanahan 2001), elle me paraît en partie justifiée par les remarques précédentes. En effet, la microévolution et en particulier la génétique des populations et la génétique quantitative utilisent largement l'expérimentation ou l'observation, et ont donc des preuves beaucoup plus directes à l'appui de leur théorie.

Avec le développement des techniques de séquençage de l'ADN, la phylogénie moléculaire est devenue l'outil principal de la macroévolution (Pagel 1999). La phylogénie décrit les relations de parenté entre différents taxons sur la base des différences dans leurs séquences d'ADN. C'est une information primordiale pour en reconstituer l'histoire : elle fournit non seulement les relations de parenté entre les taxons qui le composent, mais aussi les temps de divergence entre lignées. Ainsi, la donnée d'un modèle d'évolution (souvent une équation différentielle qui décrit le changement d'un trait au cours du temps) et d'une phylogénie permet de calculer les différences de trait attendues entre espèces actuelles. En inversant ce processus, il est possible à partir des traits des espèces actuelles d'en déduire les paramètres les plus probables du modèle d'évolution du trait (Figure 4). Bien qu'ayant utilisé des phylogénies tout au long de ma thèse, je tiens à mentionner que je n'en ai jamais construite aucune.

3.2. La niche climatique : un objet difficile à manipuler en macroévolution

La niche climatique d'une espèce est un trait assez différent de ceux couramment étudiés en macroévolution (comme les traits morphologiques), ce qui en complique l'étude. En effet, même s'il est possible de déterminer la niche d'un individu ou d'un génotype en mesurant sa fitness dans une large gamme de climats, une telle mesure est difficile à obtenir et la niche est le plus souvent utilisée comme caractéristique d'une espèce. Puisque tous les individus d'une même espèce ne peuvent généralement pas survivre dans les mêmes conditions environnementales, la niche climatique telle qu'elle est mesurée habituellement est donc un trait émergent au niveau de l'espèce (Vrba & Gould 1986), qui agrège les niches des individus qui la constituent.

De plus, la grande majorité des modèles utilisés pour décrire l'évolution d'un trait sur

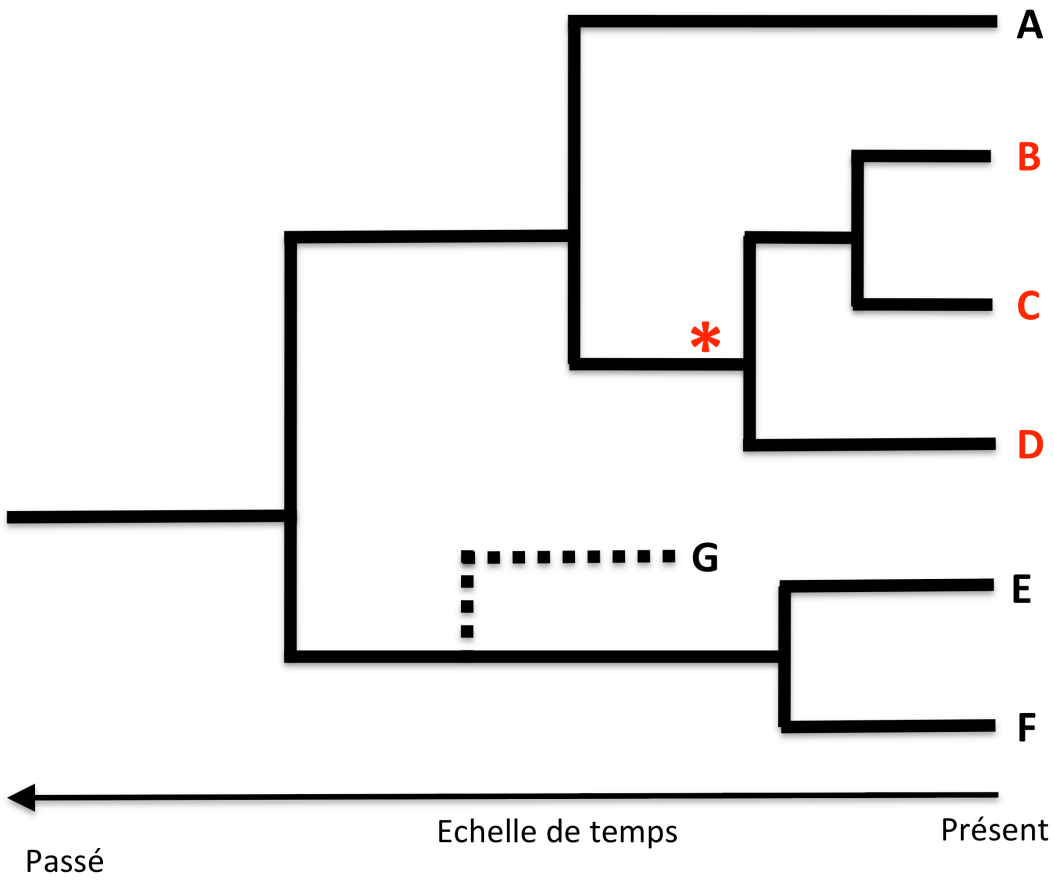

Figure 4. Phylogénie et inférences sur l'évolution des caractères. Ce schéma montre les différentes composantes de la phylogénie d'un groupe de six espèces vivant actuellement (A-F). L'axe des abscisses représente le temps, du présent (à droite) jusqu'à l'apparition du dernier ancêtre commun à toutes les espèces du groupe (à gauche, aussi appelé racine de l'arbre). La longueur de chaque branche (ligne horizontale) représente la durée de vie d'une espèce (éteinte ou actuelle). Les segments verticaux symbolisent les évènements de spéciation qui correspondent à la séparation de deux espèces 'filles' depuis un ancêtre commun. L'espèce G s'est éteinte sans laisser de descendants, elle n'est le plus souvent pas incluse dans la phylogénie car son existence est ignorée si aucun fossile n'est connu. Sur les six espèces vivantes, 3 sont noires et 3 sont rouges. Cependant, si l'on fait l'hypothèse que le scénario le plus probable est celui qui requiert le moins de changements de couleur (méthode de la parcimonie), la phylogénie nous permet d'estimer que l'ancêtre du groupe était très probablement noir et que la couleur rouge n'est apparue qu'une seule fois chez l'ancêtre commun à B, C et D (étoile rouge).

une phylogénie (voir chapitre 1 de ma thèse pour une présentation de ces modèles) s'intéressent au trait moyen de chaque espèce. En conséquence, les études d'évolution de la niche climatique utilisent souvent la niche moyenne d'une espèce sur un ou plusieurs gradients climatiques, c'est-à-dire la moyenne d'une variable climatique sur l 'ensemble de l'aire de distribution d'une espèce. Cette représentation permet de discriminer les niches de différentes espèces mais perd une grande partie de

l'information sur la niche climatique d'une espèce: l'étendue de sa tolérance climatique. Cette limitation est pour le moment difficile à contourner en analyse comparative (voir cependant Evans et al. 2009, Boucher et al. 2012) et doit donc être gardée à l'esprit.

3.3. Le conservatisme de niche phylogénétique : un concept central largement débattu

L'étude de l'évolution des niches sur des temps longs est basée sur un concept central : le conservatisme de niche phylogénétique (PNC). Le PNC a été défini par Harvey & Pagel (1991) comme 'la tendance des espèces à garder leurs principales caractéristiques écologiques au cours du temps'. Si le terme a été largement repris depuis dans la littérature (Table 1), cette définition très vague a également créé beaucoup de confusion et de débat.

Période	**Nombre d'articles**
1990-1999	11
2000-2009	199
2010-2013	356

Table 1. Nombre d'articles publiés avec 'niche conservatism' comme sujet (source : ISI web of Knowledge, 8 juillet 2013).

Le PNC : processus ou patron ?

Certains considèrent le PNC comme un processus actif qui contraint les niches à rester stables au cours du temps (Wiens 2008, Wiens et al. 2010). Ce processus peut être créé par différents mécanismes sous-jacents, et il créé des patrons d'ordre supérieur comme les gradients de diversité par exemple (Wiens 2008). A l'inverse, certains auteurs ont proposé de considérer le PNC comme un patron, justement puisque différents processus peuvent le causer (Losos 2008, Crisp & Cook 2012) et puisque la phylogénie d'un clade n'est elle-même qu'un patron créé par l'histoire de ce clade (Losos 2011). Dans la suite

de ce manuscrit, je considérerai le PNC comme un patron, puisque cela a l'avantage de souligner la nécessité d'en rechercher les causes. Les processus pouvant causer le PNC sont en effet de nature très différente et comprennent des causes directes (sélection stabilisante, héritabilité forte, manque de variabilité génétique, asymétries démographiques entre populations du cœur de la niche et populations marginales) et des causes indirectes (limitations de dispersion, compétition), qu'il me paraît nécessaire de distinguer (Figure 5).

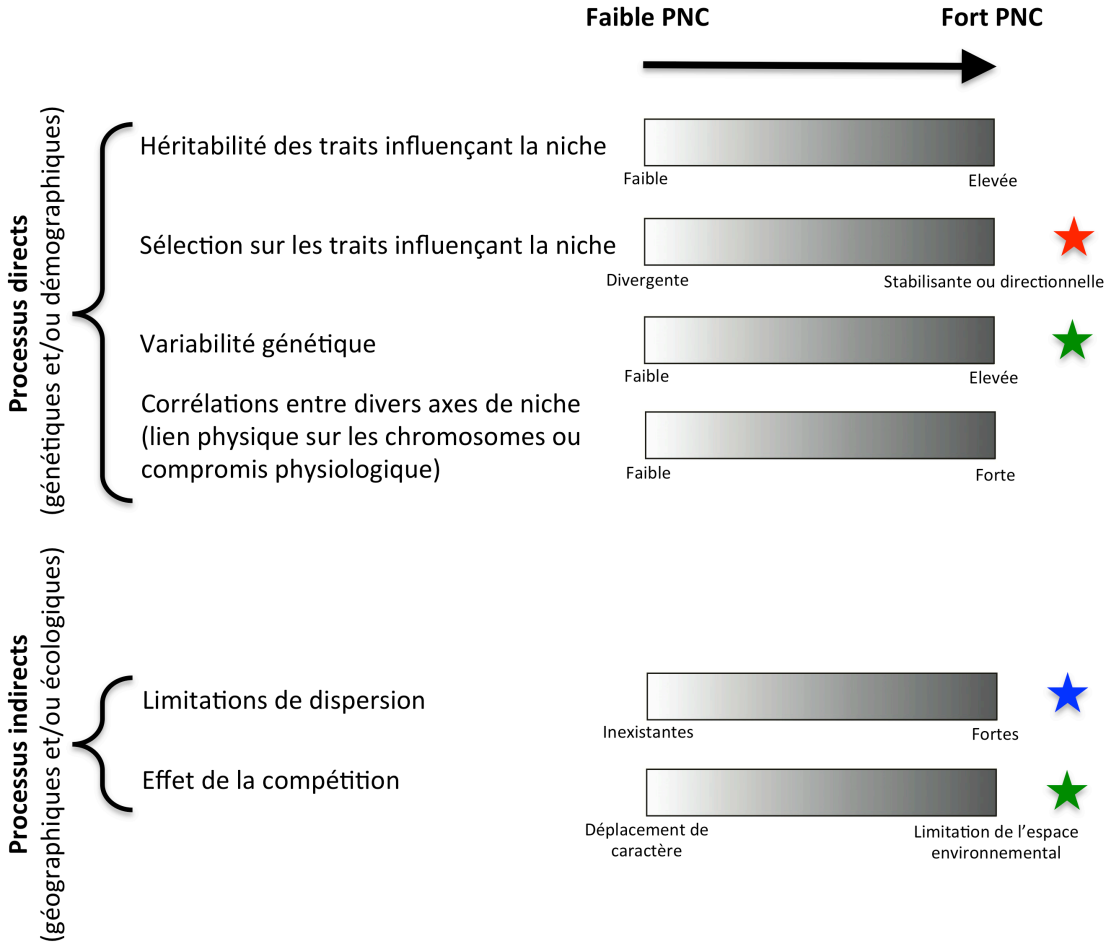

Figure 5. Causes du conservatisme de niche phylogénétique, inspiré de Crisp & Cook 2012. Les étoiles indiquent les processus que j'ai pu étudier dans ma thèse: (i) à travers un modèle de simulation en bleu (Chapitre I) ; (ii) grâce à une méta-analyse en vert (Chapitre II) et (iii) dans l'étude de cas sur le genre *Androsace* en rouge (Chapitre III).

Comment mesurer le PNC?

De très nombreuse méthodes ont été proposées pour étudier le PNC, mais deux d'entre elles sont les plus fréquemment utilisées : (i) d'un côté, l'étude des taux d'évolution fait l'hypothèse que les niches climatiques dérivent au cours du temps et utilise la vitesse de cette dérive pour mesurer le PNC (Ackerly 2009) ; (ii) la principale alternative consiste à tester la présence de PNC en comparant la vraisemblance d'un modèle de dérive à celle d'un modèle ou l'évolution de la niche est contrainte autour d'un optimum donné (Cooper et al. 2010, Wiens et al. 2010). Ces deux méthodes diffèrent fondamentalement sur leur conception du PNC : en effet, les taux d'évolution donnent une mesure relative du PNC (évolution de la niche plus rapide dans certains clades que dans d'autres) alors que les comparaisons de modèles fournissent une réponse catégorique (présence de PNC ou pas). Au-delà de ces deux méthodes principales, de nombreuses autres alternatives existent, qu'il est difficile de concilier puisqu'elles ne s'accordent pas sur une même conception du PNC.

Le PNC est-il répandu dans la nature?

Certains auteurs ont affirmé que les niches des espèces étaient très labiles en se basant sur le nombre croissant de radiations adaptatives détectées (Losos 2008). Cependant, le nombre de radiations adaptatives (radiations explosives avec forte diversification écologique associée, Schluter 2000, Losos & Mahler 2010) pourrait bien constituer un biais de publication puisque ces cas sont particulièrement impressionnants et permettent de répondre à de nombreuses autres questions en biologie évolutive (voir le nombre de publications sur les lézards du genre *Anolis*, Losos 2009, les cichlidés des grands lacs d'Afrique de l'Est, Kocher 2004, ou les pinsons de Darwin, Grant 2009). A l'opposé, certains auteurs considèrent que le PNC est omniprésent dans la nature et vont même jusqu'à en faire un 'principe émergent en écologie' (Wiens et al. 2010). Cette conception se base sur le fait que les changements de biome sont très rares (Crisp et al. 2009) et aussi sur l'observation que les espèces proches ont souvent des niches semblables. Cependant, cette vision est également biaisée puisque les changements de biome représentent des évènements majeurs qui ne sont pas représentatifs de la majorité des changements de niche (comme par exemple ceux qui sont requis par le

changement climatique actuel, bien moindres). De plus, chez les partisans du 'tout conservé' il est parfois difficile de voir la différence faite entre PNC et héritabilité génétique de la niche, même faible (Wiens et al. 2010). Si l'équation est faite entre ces deux notions, alors le PNC devient un concept inutile puisque l'héritabilité des traits est connue depuis Darwin (1859) et qu'elle a une définition bien plus précise.

3.4. Principaux enjeux sur l'évolution des niches climatiques

Clarifier la méthodologie utilisée

Comme nous l'avons vu plus haut, des méthodes très diverses sont utilisées pour étudier l'évolution des niches climatiques et mesurer le PNC et le développement de nouvelles méthodes comparatives se poursuit à un rythme effréné (Struwe et al. 2011, Beaulieu et al. 2012, Diniz-Filho et al. 2012, Ingram & Mahler 2013). Ces méthodes reposent sur divers modèles qui font des hypothèses différentes sur la façon dont les niches évoluent. Alors que des cadres méthodologiques pour l'étude du PNC ont été suggérés (Cooper et al. 2010, Wiens et al. 2010), peu d'études ont étudié les conséquences d'un mauvais choix de modèle évolutif (voir cependant Revell et al. 2008, Münkemüller et al. 2012), et surtout l'adéquation des modèles à la question posée.

Il est donc impératif d'étudier en détail le comportement des différentes méthodes utilisées pour étudier l'évolution des niches climatiques, afin de mieux comprendre leurs biais et de voir lesquelles sont les plus robustes aux violations d'hypothèses.

Faire le lien avec les processus sous-jacents

Les modèles utilisés en macroévolution sont très largement phénoménologiques : ils ne visent pas à décrire explicitement les processus sous-jacents d'évolution, mais plutôt à en capturer les grandes caractéristiques. La façon dont différents processus agissant au niveau des individus influence l'évolution des niches climatiques reste largement inexplorée. Si la dérive génétique et la sélection ont été un peu étudiées (voir Revell et al. 2008), l'influence des autres processus écologiques qui déterminent la niche, comme les interactions biotiques ou la dispersion n'a jamais été examinée. La distinction entre

niche fondamentale et réalisée a souvent été passée sous silence dans les études sur l'évolution des niches climatiques (voir cependant Wiens & Graham 2005). Ceci est problématique puisqu'il est probable que les traits physiologiques, ceux qui déterminent ou sont influencés par les interactions biotiques et ceux qui déterminent les capacités de dispersion n'évoluent pas de la même façon ni au même rythme. De plus, les limites de dispersion ne sont qu'en partie déterminées par les capacités de dispersion des individus, mais sont surtout influencées par l'environnement physique des individus (barrières géographiques, couloirs d'habitat favorable permettant la migration, etc.).

Des études théoriques de l'influence de la compétition entre individus ou de la dispersion sur la manière dont les niches climatiques évoluent sur de grandes échelles de temps sont donc requises afin de pouvoir interpréter correctement les résultats des études empiriques.

Caractériser de mode d'évolution des niches climatiques et mesurer la fréquence du PNC dans la nature

Savoir si les niches climatiques sont généralement conservées ou si elles sont capables d'évoluer facilement est une question primordiale. L'évolution des niches climatiques a également des implications pour les la biogéographie historique (Wiens & Donoghue 2004, Jablonski et al. 2006), les invasions biologiques (Petitpierre et al. 2012) et la réponse des espèces au changement climatique (Lavergne et al. 2010, Salamin et al. 2010).

Pour cela, il est d'abord nécessaire de caractériser le mode d'évolution des niches climatiques, c'est-à-dire la façon dont elles évoluent (Simpson 1953). La conception généralement admise depuis Darwin (1859) est que les traits évoluent de manière lente et graduelle. Au contraire, la théorie de l'équilibre ponctué postule que des phases d'évolution rapide ont lieu durant les évènements de spéciation alors que les traits restent plutôt stables au cours de la vie des espèces (Gould & Eldredge 1977). Enfin, que l'évolution des niches climatiques soit graduelle ou ponctuelle, il est important de savoir si les niches subissent des contraintes (Maynard-Smith et al. 1985, Arnold 1992) ou alors si elles évoluent librement dans n'importe quelle direction. Déterminer le mode d'évolution des niches climatiques le plus répandu dans la nature (s'il existe) permettra

non seulement d'en identifier les causes les plus probables mais aussi de choisir des modèles adaptés pour étudier la fréquence du PNC.

Malgré le nombre croissant de cas d'étude qui ont été publiées sur l'évolution des niches climatiques (Table 1), les différences de méthodologie ou de données employées empêchent pour l'instant de faire un bilan quantitatif des connaissances sur l'évolution des niches climatiques et en particulier sur la fréquence du PNC. Il est donc urgent d'étudier l'évolution des niches climatiques dans de nombreux groupes dans un cadre méthodologique robuste.

4. La Flore alpine : contexte, intérêt comme cas d'étude et enjeux.

L'objectif final de ma thèse était d'étudier l'évolution des niches climatiques et de la distribution des espèces végétales alpines. Ce travail est nécessaire car les environnements alpins ont été relativement peu étudiés en biologie évolutive et parce que les espèces alpines sont particulièrement menacées par le changement climatique puisqu'un réchauffement condamnerait nombre d'entre elles à l'extinction, sans possibilité de migration vers les régions arctiques qui sont assez éloignées (Engler et al. 2009, McCain & Colwell 2011, Dullinger et al. 2012).

4.1. Caractéristiques générales des environnements alpins et conséquences sur la végétation

Dans la suite de ce manuscrit, nous retiendrons la définition des environnements alpins fournie par le Global Moutain Biodiversity Assessment (http://gmba.unibas.ch/): ce sont des environnements au relief accidenté et situés au dessus de la limite supérieure potentielle des arbres, ce qui correspond à une saison de végétation de moins de 94 jours par an et à une température moyenne pendant la saison de végétation inférieure à +6.4°C (Körner et al. 2011). A l'échelle du globe on distingue deux grands types d'habitats alpins (Figure 6). Les habitats alpins tempérés comprennent l'ensemble des massifs qui bordent le sud de l'Eurasie (des Pyrénées à L'Himalaya, incluant les Alpes), les montagnes Rocheuses en Amérique du Nord, le sud des Andes et les Alpes Néo-zélandaises. Ces environnements sont caractérisés par des températures extrêmement froides, qui obligent la végétation à se protéger du gel en adaptant diverses stratégies, comme par exemple un port dense qui protège les bourgeons du froid et permet également de limiter les pertes d'eau (comme la forme de vie en coussin, cf. Chapitres 3 & 4) ou encore en produisant des métabolites qui abaissent le point de congélation des cellules (Streb et al. 2003). Enfin, la présence de neige pendant de nombreux mois exerce de fortes contraintes sur la végétation : elle interdit aux plantes de trop pousser en hauteur sous peine de voir leurs tiges casser et réduit la saison de végétation à quelques mois entre la fin du printemps et le début de l'automne.

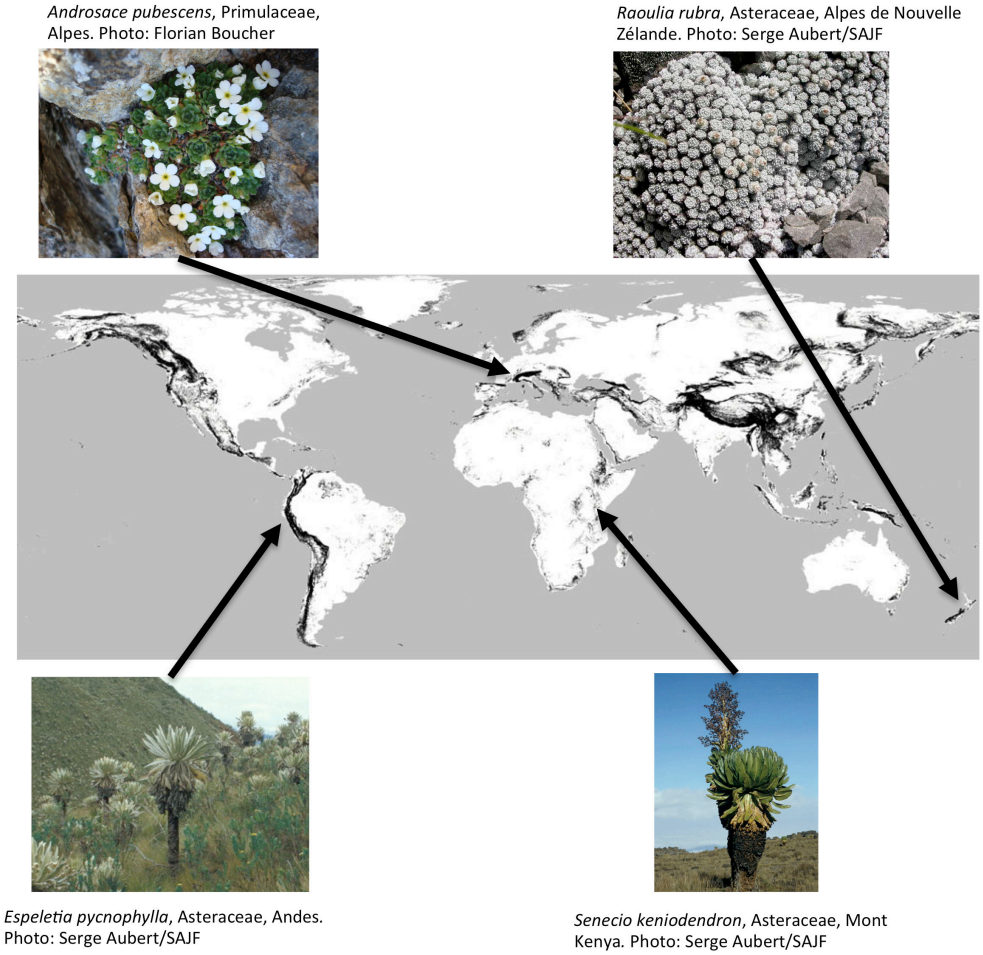

Figure 6. Les montagnes du monde et leur flore. Cette carte montre les régions montagneuses du monde (en noir, d'après Körner et al. 2011). En haut: deux plantes en coussin, typiques des environnements alpins tempérés. En bas: deux plantes pachycaules, typiques des environnements alpins tropicaux.

A l'opposé, les habitats alpins tropicaux que l'on rencontre dans les Andes, les montagnes d'Afrique de l'Est et en Papouasie-Nouvelle-Guinée, sont soumis à de fortes oscillations de température journalières. Dans ces environnements, les nuits peuvent être très froides mais la neige tient rarement plusieurs jours (Körner 1999). Les plantes pachycaules, qui dominent souvent les paramos de la zone alpine tropicale (e.g. *Espeletia, Puya* ou *Lupinus* dans les Andes, *Senecio* ou *Lobelia* en Afrique de l'Est), fournissent un bon exemple d'adaptation à ces conditions. Chez les plantes du genre *Espeletia* par exemple, le bourgeon terminal est entouré par une dense rosette de feuilles : ce système est efficace pour protéger le bourgeon du gel pendant quelques heures mais permet au métabolisme de reprendre rapidement dès que la température

extérieure le permet (Monasterio et al. 1995).

En plus du stress thermique que nous venons d'évoquer, les environnements alpins sont soumis à d'autres contraintes environnementales, comme des radiations solaires intenses, de forts vents et la pauvreté des sols.

4.2. Les espèces alpines : un modèle privilégié pour étudier l'évolution des niches climatiques

Les systèmes alpins sont un modèle privilégié pour étudier l'évolution des niches climatiques pour deux raisons principales : la faible importance de la compétition interspécifique et la fragmentation de l'habitat.

Le climat est le principal déterminant de la distribution des espèces alpines, du moins détermine-t-il généralement la limite 'froide' de leur distribution (Körner 1999, Boulangeat et al. 2012). En comparaison, la compétition entre plantes est moins importante dans les milieux alpins : ceci a été démontré au niveau des communautés (hypothèse du gradient de stress, Callaway & Walker 1997, Lortie & Callaway 2006) et le filtre environnemental a également été évoqué pour expliquer la variabilité des traits fonctionnels extrêmement réduite dans les populations de *Polygonum viviparum* situées en haute altitude (Boucher et al. 2013). Même si des processus de facilitation ont été documentés dans les communautés alpines (Callaway et al. 2002, mais voir De Bello et al. 2011 pour un contre exemple), les interactions biotiques paraissent donc moins importantes que les contraintes abiotiques. Ceci nous permet de nous rapprocher des hypothèses des modèles utilisés en macroévolution, qui ne prennent pas en compte les interactions entre espèces.

Les environnements alpins ont également l'avantage d'être des systèmes insulaires. En effet, les sommets montagneux forment diverses 'îles environnementales' (Ackerly 2003) sont souvent isolées les unes des autres par des vallées au climat moins stressants (Figure 6). Même si ces archipels d'habitats alpins sont moins clairement délimités que leurs homologues des mers ou des océans, ils sont néanmoins assez faciles à délimiter. Cette configuration permet de dresser des parallèles avec la théorie de la

biogéographie insulaire (Mc Arthur & Wilson 1969) et d'en utiliser certains concepts, comme la colonisation de régions périphériques depuis un 'continent' ou encore la relation entre aire et nombre d'espèces.

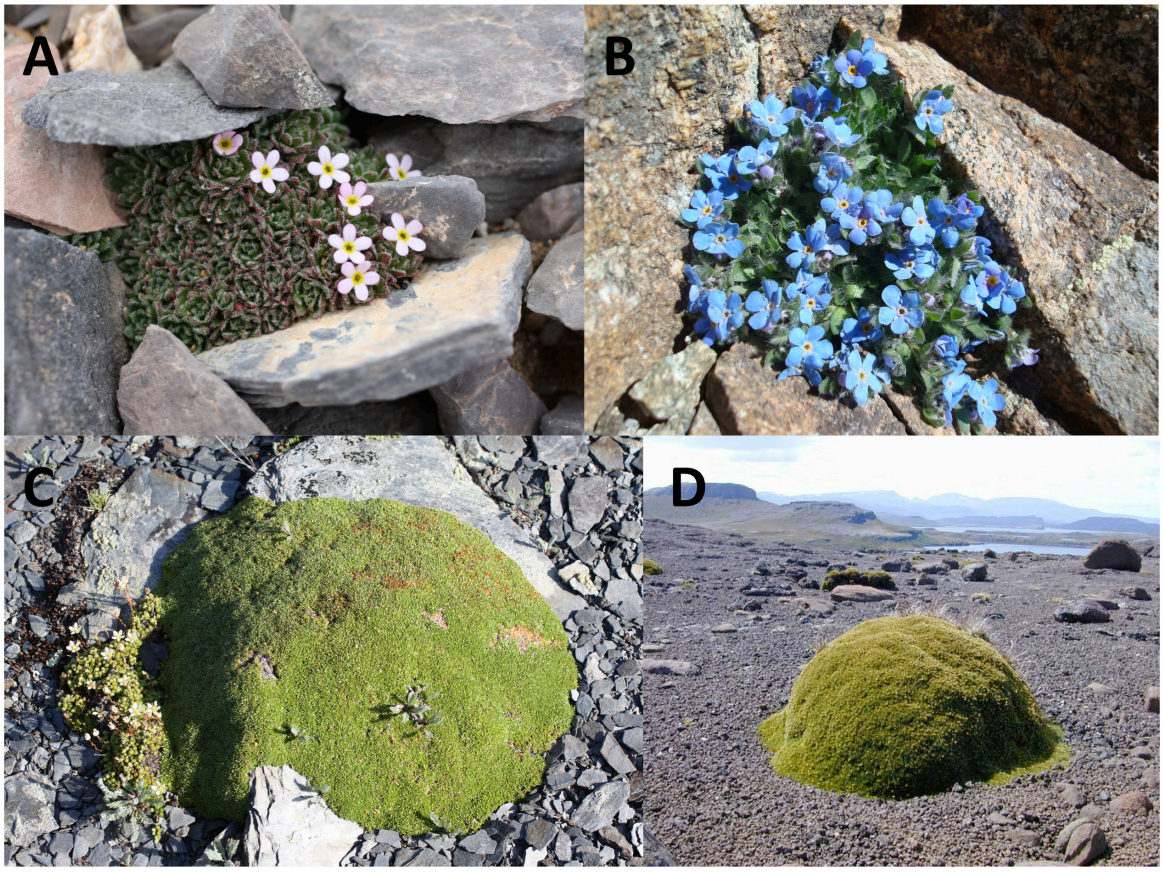

Figure 7. Exemples de plantes en coussin. A. *Androsace alpina* (Primulaceae), endémique des Alpes. B. *Eritrichium nanum* (Boraginaceae), présente dans les Alpes, les Carpates et les Montagnes Rocheuses. C. A gauche (avec des fleurs blanches): *Saxifraga exarata subsp. moschata* (Saxifragaceae), présente dans les Alpes, le Jura et les Apennins; à droite: *Silene acaulis* (Caryophillaceae), distribution Holarctique. D. *Azorella selago* (Apiaceae), présente dans les régions australes. Comme le montrent ces photographies, les plantes en coussin occupent souvent des habitats pauvres et poussent à même le rocher. Le panneau C illustre la facilitation parfois réalisée par les plantes en coussins: on peu distinguer quelques individus d'*Achillea nana* dans le coussin de *S. acaulis.* Photos A-C: F. Boucher ; D: S. Aubert/SAJF.

4.3. Les plantes en coussin, emblèmes de la flore alpine

Parmi les plantes alpines, je me suis plus particulièrement intéressé aux plantes en coussins. La forme de vie en coussin est un type d'architecture végétale que possèdent

en effet de très nombreuses espèces de plantes alpines dans le monde (voir Figure 7). Elle est caractérisée par un port compact dû à de nombreuses ramifications et à un raccourcissement des entrenœuds. Cette structure permet de tamponner les variations de températures et d'humidité à l'intérieur de la plante (Larcher 2010). Les coussins constituent une part importante de la flore des environnements alpins et arctiques du globe, dont ils sont des éléments structurants. En effet, ce sont de véritables ingénieurs des écosystèmes, qui modifient les conditions locales et facilitent l'installation et/ou la survie de certaines plantes en leur sein (Callaway et al. 2002, Figure 7C), augmentant ainsi la diversité locale (Butterfield et al. 2013).

4.4. Questions principales pour l'étude des origines de la Flore alpine

Retracer l'histoire de l'adaptation aux environnements alpins

Les habitats alpins sont relativement jeunes à l'échelle de l'histoire du vivant : ils seraient apparus il y a moins de 50 millions d'années (Fine & Ree 2005). La totalité des grands groupes d'êtres vivants est donc apparue sous des climats tropicaux et y a passé la majeure partie de son histoire évolutive. Les espèces alpines ont dû s'adapter à des environnements extrêmes sur une durée relativement courte.

Etudier comment cette adaptation aux climats alpins s'est réalisée permettra de comprendre le rôle des pressions sélectives qui ont probablement accompagné les orogénèses, mais aussi celui de l'isolation géographique entre différents massifs. Enfin, le rôle joué par certains traits dans l'évolution des niches climatiques devrait pouvoir être mis en évidence.

La diversité des environnements alpins: un patron clair qui va à l'encontre de nombreuses attentes

Dans leur ensemble, les environnements alpins ne représentent que 2.6% de la surface du globe (Körner et al. 2011) mais abritent une part importante de la biodiversité terrestre, tant faunistique que floristique (Orme et al. 2005, McCain & Colwell 2011).

Une telle diversité est étonnante pour plusieurs raisons.

Tout d'abord, la formation relativement récente des environnements alpins leur a donné moins de temps pour accumuler des espèces que les environnements tropicaux et tempérés. De plus, l'isolation relative des régions alpines fait que la migration d'espèces entre massifs devrait faiblement contribuer à leur diversité. Les fortes perturbations climatiques qu'on connus les environnements alpins, comme les glaciations, pourraient également avoir entraîné l'extinction de nombreuses espèces, au moins localement (Brown & Lomolino 1998). Finalement, la pauvreté des milieux alpins voudrait que la diversité y soit faible. En effet, de nombreux travaux théoriques et empiriques suggèrent que les milieux où l'énergie est abondante permettent de créer et de maintenir une plus grande diversité que les milieux pauvres en énergie (Currie et al. 2004, Storch et al. 2006). La théorie métabolique de l'écologie a en effet établi l'effet de la température sur les processus biochimiques cellulaires (Gillooly et al. 2001, Brown et al. 2004), conduisant en particulier à des taux d'évolution moléculaire plus élevés sous les climats tropicaux et donc potentiellement à des taux de spéciation plus élevés (Allen et al. 2006). Des études empiriques ont ensuite confirmé que les espèces tropicales spécient plus vite que leurs congénères vivant sous des climats tempérés, du moins dans certains groupes (Cardillo 1999, Wright et al. 2006, Duchene & Bromham 2013).

Face à ce paradoxe apparent, il est important d'étudier l'histoire de la biodiversité alpine afin de comprendre pourquoi les environnements alpins sont si riches malgré ces différents facteurs *a priori* défavorables.

5. Plan du manuscrit

Au cours de ma thèse, j'ai essayé d'apporter des réponses aux grands enjeux scientifiques présentés plus haut, d'une part en ce qui concerne l'évolution des niches climatiques des espèces, puis sur la connaissance des origines de la Flore alpine. Pour répondre à ces questions, ce manuscrit est divisé en quatre chapitres.

Le premier chapitre est purement théorique et constitue une étape nécessaire avant d'aborder les cas d'études dans les parties suivantes. Tout d'abord, nous avons testé les performances et la pertinence des différentes méthodes communément utilisées pour étudier le PNC (article 1.1). Ensuite, en utilisant des simulations numériques, nous avons étudié les patrons d'évolution des niches climatiques produits par un scénario purement neutre où des individus migrent dans le paysage et sont en compétition pour l'espace, sans qu'aucune force sélective n'agisse (article 1.2).

Le second chapitre de ma thèse vise à déterminer la manière dont les niches climatiques évoluent généralement dans la nature. Pour cela, nous avons assemblé un large jeu de données. En utilisant une vaste panoplie de modèles macroévolutifs, nous avons d'abord tenté de révéler le mode d'évolution le plus fréquent des niches climatiques. Nous avons ensuite mesuré le degré de PNC dans chaque clade, ce qui nous a permis de fournir des éléments de réponse sur la fréquence du PNC dans la nature. Enfin, nous avons cherché à révéler les causes principales du PNC, parmi celles qui ont été évoquées dans la littérature (article 2).

Dans le troisième chapitre, nous avons tenté de décrypter l'histoire évolutive du genre *Androsace* L., un genre de plantes présent dans toutes les zones tempérées, arctiques et alpines de l'hémisphère Nord et qui compte des espèces parmi les plus endurantes au froid chez les angiospermes. Nous avons d'abord étudié l'apparition de la forme de vie en coussin chez *Androsace* et son impact sur l'évolution des niches climatiques dans le genre (article 3.1). Ensuite, nous avons examiné les conséquences de l'apparition des espèces alpines en étudiant la biogéographie du genre *Androsace* ainsi que sa diversification (article 3.2). L'étude d'*Androsace* nous a permis de mieux comprendre les mécanismes généraux ayant conduit à la formation de la flore alpine des régions tempérées.

Finalement, le quatrième chapitre de ma thèse constitue une prise de recul et s'est intéressé à des échelles phylogénétiques et biogéographiques beaucoup plus larges. Nous y avons en effet étudié l'histoire de la forme de vie en coussin dans l'ensemble des Angiospermes et montré que c'était une convergence évolutive très largement répandue (article 4.1). Ensuite, en combinant analyses macroévolutives et biogéographiques, nous avons cherché à comprendre les causes climatiques, historiques et biogéographiques de l'apparition des coussins et de leur distribution actuelle à l'échelle globale (article 4.2).

Chaque chapitre s'ouvre sur une introduction au contexte et aux questions abordées. Les principaux résultats obtenus sont ensuite résumés, avant la présentation des articles scientifiques qui constituent le cœur de chaque chapitre.

Ce manuscrit se conclut par une discussion des principaux résultats obtenus. Nous y ferons le lien entre les différents chapitres et verrons comment ils s'éclairent mutuellement. Nos contributions à la problématique de l'évolution des niches climatiques seront aussi présentées. Finalement, je proposerai des perspectives personnelles sur les développements récents et à venir de la macroévolution.

CHAPITRE 1.

COMMENT ETUDIER L'EVOLUTION DES NICHES CLIMATIQUES ?

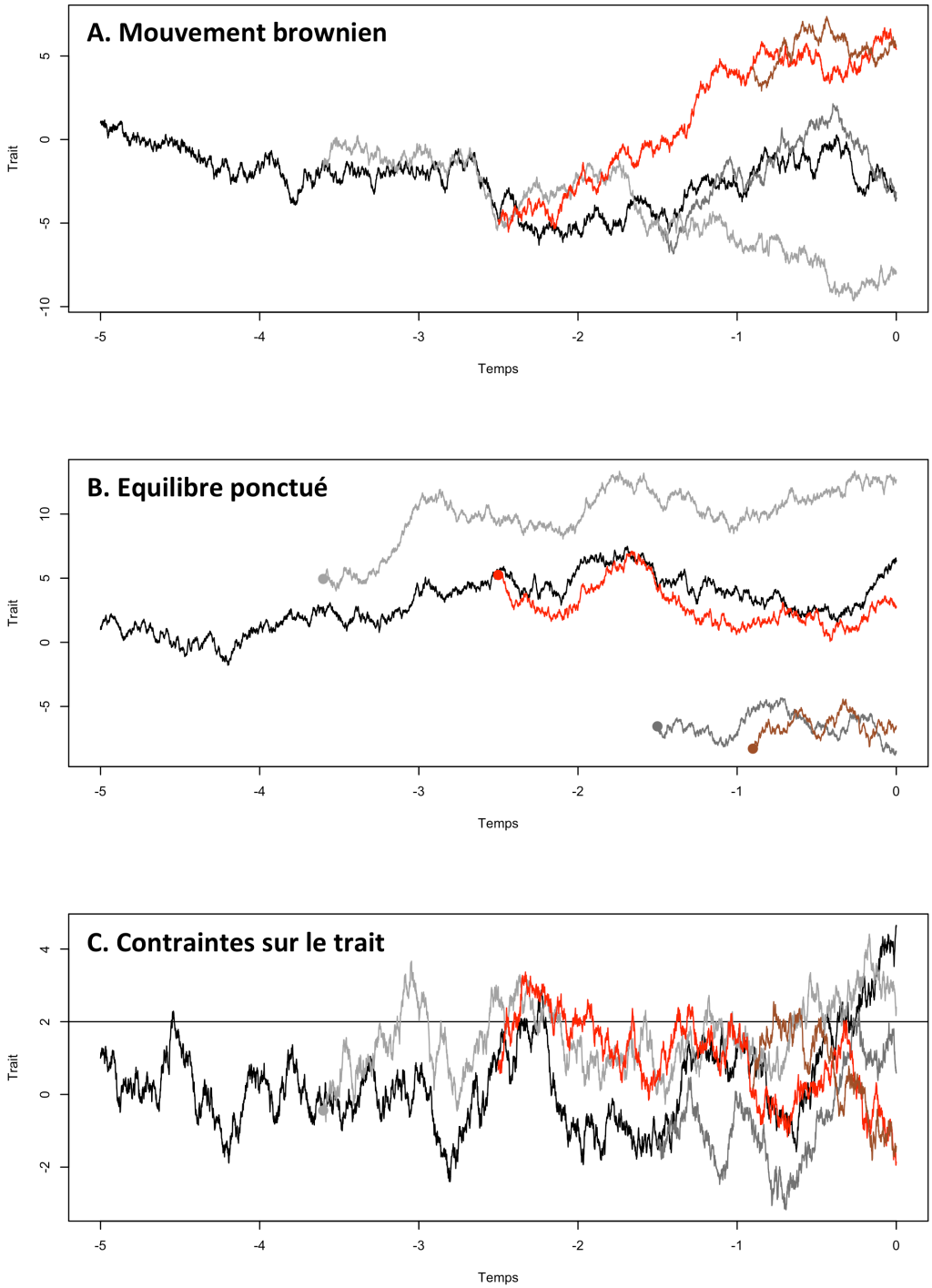

Figure 8. Trois modèles principaux d'évolution des traits continus. Les traits de cinq espèces sont représentées au cours du temps. A. Mouvement brownien: les traits dérivent au cours du temps sans direction privilégiée et à une vitesse constante. B. Equilibre ponctué: les traits dérivent au cours du temps mais évoluent surtout grâce à des grands sauts à la spéciation. C. Modèle d'Ornstein-Uhlenbeck: les traits dérivent mais sont également attirés par une valeur optimale (ligne horizontale).

Introduction

Dans ce premier chapitre j'ai choisi de traiter certains aspects méthodologiques (article 1.1.) et conceptuels (1.2.) de l'étude de l'évolution des niches climatiques des espèces. Dans tous les modèles qui suivent, la phylogénie d'un groupe d'espèces (un clade) est fixée et considérée comme parfaitement connue. Les modèles qui sont décrits plus bas permettent tous, connaissant la valeur du caractère de chaque espèce vivant actuellement, de calculer la fonction de vraisemblance de ces caractères sachant des valeurs des paramètres (la probabilité d'observer ces valeurs de traits sachant la phylogénie et les paramètres du modèle). Les valeurs des paramètres les plus plausibles sont alors estimées par maximum de vraisemblance ou en utilisant des méthodes issues des statistiques bayésiennes. Différents modèles peuvent également être comparés sur la base de leur vraisemblance, le plus souvent en utilisant l'AIC (Akaike 1974).

Le Mouvement Brownien

Le modèle du Mouvement Brownien a été adopté par la macroévolution pour étudier l'évolution des traits continus (Edwards & Cavalli-Sforza 1964, Felsenstein 1985). Dans ce modèle, le trait X d'une espèce dérive au cours du temps à une vitesse constante, sans direction privilégiée et sans influence des autres espèces (Figure 8A). Ceci est formalisé par l'équation différentielle suivante :

$$X(t + dt) = X(t) + dB(0, \sigma^2 . dt) \quad (1)$$

Dans cette équation, $dB(0, \sigma^2 . dt)$ suit une loi normale de moyenne 0 et de variance σ^2dt. σ est le seul paramètre du modèle et décrit la vitesse de la dérive du trait, il est souvent appelé 'taux d'évolution' du trait (Ackerly 2009). En raison de sa simplicité, le Mouvement Brownien est très utilisé en macroévolution et sert toujours de modèle nul contre lequel tester des modèles plus complexes. Sous un Mouvement Brownien, la variance d'un trait augmente linéairement avec le temps. Ainsi, plus deux espèces sont apparentées (plus elles ont divergé récemment), plus leurs traits sont similaires. C'est cette prédiction que teste le signal phylogénétique (voir article 1.1.). Si le Mouvement Brownien a été développé pour

modéliser la dérive sur des échelles de temps longues, soulignons qu'il peut aussi être interprété comme de la sélection dans un environnement fluctuant.

L'équilibre ponctué

S'il est moins connu des phylogénéticiens, l'équilibre ponctué est un modèle incontournable chez les paléontologues. Ce modèle a en effet été introduit par Gould & Eldredge (1977) pour expliquer les brusques changements de traits qui sont observés lors des évènements de spéciation dans les archives fossiles. Ainsi, d'après ce modèle, les traits restent relativement stables entre deux évènements de spéciation (stase) mais changent rapidement lors de la spéciation (ponctuation, Figure 8B). Cette évolution ponctuée s'oppose au mode d'évolution graduel, comme c'est le cas dans le Mouvement Brownien. Le premier à tester ce mode d'évolution sur des phylogénies a été Pagel (1994), qui a utilisé le fait que lorsqu'un trait évolue de façon ponctuée, sa variance augmente (surtout) avec le nombre de spéciations et non pas avec le temps. Bokma (2008) a ensuite repris ces travaux et formalisé un modèle où le trait X d'une espèce subit deux types d'évènements. Entre deux spéciations, le trait suit un Mouvement Brownien de taux σ_a :

$$X(t + dt) = X(t) + dB(0, \sigma^2 . dt) \quad (2.1)$$

Mais à la spéciation, le trait des deux espèces filles subit un changement instantané tiré dans une loi normale de moyenne 0 et de variance σ_c^2 :

$$X(espèce\ fille) = X(espèce\ mère) + dB(0, {\sigma_c}^2) \quad (2.2)$$

Bien sûr, le caractère instantané du changement de trait entre espèces mère et filles ne doit pas être interprété au pied de la lettre. L'équilibre ponctué traduit plutôt le fait que les changements de trait se produisent autour de la spéciation ou même pendant qu'elle se déroule (Gould 2002).

Le modèle d'Ornstein-Uhlenbeck

Afin de modéliser la sélection stabilisante, Hansen (1997) a introduit le modèle d'Ornstein-Ulhenbeck (OU dans la suite). Dans ce modèle, en plus de la dérive, le trait subit une force de rappel vers une valeur optimale. Comme dans le cas d'un ressort en physique, plus le trait est éloigné de cette valeur optimale, plus la force de rappel est grande. Ainsi, sous l'effet conjoint de la dérive et de la sélection, le trait X d'une espèce oscille autour de la valeur optimale mais n'y reste pas à l'équilibre (Figure 8C) :

$$X(t + dt) = X(t) + \alpha(\theta - X(t)) \ + dB(0, \sigma^2.dt) \quad (3)$$

Dans cette équation, on reconnaît encore le terme du Mouvement Brownien et deux nouveaux paramètres sont introduits : θ est la valeur optimale vers laquelle le trait est rappelé et α est l'intensité de cette force de rappel. Même s'il a été proposé pour modéliser la sélection stabilisante sur des échelles de temps macroévolutives, le modèle OU peut représenter la présence de contraintes, qu'elle que soit leur nature. En particulier, ce modèle ressemble beaucoup à un Mouvement Brownien borné (voir article 1.2.).

En se basant sur les modèle simples que nous venons de présenter, des modèles plus complexes ont été proposés, comme des modèles où le trait dérive mais à des vitesses différentes dans différents clades (O'Meara et al. 2006). Les modèles OU à plusieurs optima sont particulièrement intéressants puisqu'ils permettent de modéliser des contraintes sur le trait qui diffèrent entre clades (Butler & King 2004).

Le premier article de ce chapitre (1.1.) est encore une version très préliminaire, où la discussion n'a pas encore été entièrement rédigée. Nous y verrons comment ces différents modèles peuvent servir à mesurer le conservatisme de niche phylogénétique et surtout quelles erreurs sont à éviter. Nous soulignerons qu'il est important de bien avoir en tête les hypothèses faites par chaque modèle.

Enfin, dans le deuxième article (1.2.), je montrerai qu'un scénario totalement neutre, où des individus se reproduisent et migrent de manière aléatoire dans un paysage borné, peut conduire à une évolution ponctuelle des niches climatiques mais surtout à un modèle OU. Ce

résultat souligne que le choix d'un modèle OU par rapport à un autre modèle ne doit pas être interprété comme une preuve de sélection stabilisante en l'absence de données complémentaires sur la biologie d'un groupe.

ARTICLE 1.1

ECUEILS CONCEPTUELS ET METHODOLOGIQUES DANS L'ETUDE DU CONSERVATISME DE NICHE PHYLOGENETIQUE

Common conceptual and methodological pitfalls in the analyses of phylogenetic niche conservatism

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Abstract

1. The prevalence of phylogenetic niche conservatism (PNC) in nature is still a conflicting issue. The disagreement arises from confusion over its precise definition and the appropriate approaches to measure its prevalence. Recent work has highlighted that common measures of PNC strongly depend on the assumptions of the underlying model of niche evolution. However, this warning has not been well recognized in the applied literature and questionable approaches are still frequently applied.

2. The aim of this paper is to pinpoint the historical divergences over definitions and appropriate tests of PNC, to draw attention towards frequent biases and pitfalls of common approaches towards PNC and to clarify their relevance to applied research.

3. We demonstrate with simulated data how commonly applied approaches (phylogenetic signal, evolutionary rate, Pagel's δ, and the α parameter of a 1-optimum-Ornstein-Uhlenbeck (OU) model) do not appropriately test PNC, and can produce strongly misleading results when model assumptions are not met. Additional analyses of empirical data and examples from the literature show that these cases are frequent. Brownian motion is rarely a good approximation for the underlying niche evolution process and often highly flexible niche evolution models are chosen when compared to simple 1-optimum OU-models.

4. Assumptions of a specific niche evolution model need to be more critically taken into account, and some models should definitely be avoided as 'general tests' of PNC. In particular, the application of phylogenetic signal and Pagel's δ is questionable given that the assumption of Brownian motion is frequently not met. In general, single estimates of PNC for entire phylogenies seem inadequate as the process of niche evolution often differs between different clades of the phylogeny. We claim that studies investigating PNC should always compare alternative evolutionary models. Model comparisons should in particular include 'highly flexible niche evolution models', even though these are data hungry. The general prevalence of PNC in nature should be evaluated only based on studies keeping up to these standards.

Keywords: Ornstein-Uhlenbeck, Brownian motion, neutral drift, rates of evolution, niche lability, macro-evolutionary model

Introduction

The interplay between ecological and evolutionary processes drives biodiversity (Ricklefs 1987). A signature of these processes is contained in phylogenetic trees and in the distribution of species' traits within these trees (Webb *et al.* 2002). In order to better understand contemporary biodiversity patterns, evolutionary ecologists have started to make use of the increasing availability of trait databases and large molecular phylogenies (Bininda-Emonds *et al.* 2008; Smith & Donoghue 2008; Thuiller *et al.* 2011). One major aim is to identify the extent to which species' niches, i.e. the set of abiotic and biotic conditions favorable for population growth and stability (Hutchinson 1957), have been conserved during evolution (Wiens & Graham 2005; Wiens *et al.* 2010). Studying phylogenetic niche conservatism is important for a broad range of research questions (see Wiens & Graham 2005; Wiens *et al.* 2010 for overviews of relevant research areas). However, the ever-increasing number of studies and their contrasting results has led to (1) blurring the concept of phylogenetic niche conservatism and (2) created debate and confusion over its prevalence in nature and appropriate ways to measure and test phylogenetic niche conservatism (Cooper, Jetz & Freckleton 2010).

(1) Phylogenetic niche conservatism (hereafter PNC) originates from the observation that ecological traits among closely related species are often similar (Wiens & Graham 2005; Losos 2008; Pearman *et al.* 2008). Darwin (1859) identified the common ancestry of related species as the primary reason for the similarity of their niches. If niche relevant traits evolve according to Brownian motion (neutral drift, Edwards & Cavalli-Sforza 1964, Felsenstein 1985) then species tend to retain their ancestral niches. Grafen (1989) was the first to suggest another explanation for niche similarity of related species including not only kinship but also environmental constraints and biogeographic history. Closely related species may tend to be similar since in the past new niches were likely to be filled by species already occupying similar niches. These species could survive better initially and evolve to full niche exploitation more rapidly due to better pre-adaptation (Grafen 1989). Subsequent stabilizing selection of niche related traits in similar environments would lead closely related species to be more similar ecologically than expected under Brownian motion. An Ornstein-Uhlenbeck (OU) model, which combines a Brownian motion process with selection towards one or several optimal values, can be used to describe this niche evolution process (Hansen 1997, Butler & King 2004). Grafen's explanation was then revisited by Harvey and Pagel (1991) and termed phylogenetic niche conservatism. Later, Wiens and Graham (2005) defined phylogenetic niche conservatism as the 'tendency of species to retain ancestral ecological characteristics' (p. 519).

(2) The prevalence of PNC is strongly debated in the literature. While some studies have reported support for PNC (Ackerly 2004; Gomez, Verdu & Perfectti 2010; Burns & Strauss 2011), others have provided counter-examples (Evans *et al.* 2009; Dormann *et al.* 2010) and a number of studies have shown that it depends on studied systems, time scales and niche-related traits (Peterson, Soberon & Sanchez-Cordero 1999; Freckleton & Jetz 2009; Cooper, Freckleton & Jetz 2011). One major part of this debate is the disagreement about the best approach towards measuring PNC. Cooper et al. (2010; see also Wiens *et al.* 2010) reviewed the different approaches and related them to the underlying models of niche evolution. PNC may be measured via: (a) phylogenetic signal, i.e. the 'tendency for related species to resemble each other more than they resemble species drawn at random from the tree' (Blomberg & Garland 2002, p. 905) under the assumption of a Brownian motion model and if phylogenetic signal is not significantly lower than 1, (b) an estimate of the evolutionary rate if it is low in comparison to other clades (see Box 1 for a discussion on phylogenetic signal vs. evolutionary rate), (c) Pagel's δ (Pagel 1999) which indicates niche retention, i.e. traits are more stable in the present but changed rapidly close to the

Box 1: Phylogenetic signal vs. evolutionary rate

Losos (2008a) suggested that PNC can be measured by a pattern of phylogenetic signal that is stronger than the pattern expected under Brownian motion (neutral drift). In its original definition, phylogenetic niche conservatism implies resistance to change and hence niches that diversify relatively slowly over time, leading to reduced evolutionary rates of niche related traits (Ackerly 2009). Consequently, other authors suggested measuring PNC via estimates of the evolutionary rate in a Brownian motion model (Cooper, Jetz & Freckleton 2010). Under the assumption that the rate of evolution and phylogenetic signal are correlated, these two perspectives are in concordance. This view was widely accepted until recently (Gittleman et al. 1996; Blomberg et al. 2003). However, Revell at al. (2008) showed that there is no straightforward relation between evolutionary rate and phylogenetic signal. Under Brownian motion, increasing the rate of evolution does not change the resulting phylogenetic signal. Under an OU-model with one optimum, phylogenetic signal is very low and indicates labile niches while evolutionary rates are low and indicate PNC (Revell at al. 2008; Ackerly 2009).

The debate on these seemingly irreconcilable perspectives on PNC is a good example for the importance of paying attention to the underlying modeling assumptions. On the one hand, phylogenetic signal can only be used if niches evolved according to Brownian motion. Thus the value of phylogenetic signal has to be congruent with Brownian motion expectations and the discussion whether values higher than zero or values higher than Brownian motion expectations indicate PNC seems pointless. On the other hand, an overall evolutionary rate does not tell us anything about higher or lower than expected niche similarity of related species under a Brownian motion assumption, i.e. different evolutionary rates result in the same expectation for phylogenetic signal.

root of the phylogeny, if values are lower than 1 and under the assumption that niche evolution along a δ-transformed phylogeny follows Brownian motion (d) the α estimate in an Ornstein-Uhlenbeck model which measures the selection strength to the optimal values, if it strongly pulls towards optimal values similar to the ancestors' niches and (e) a model comparison of white noise, Brownian motion and OU-models which identifies PNC if a OU-model with few optima and high attractor strength is chosen.

It has been stated in a number of conceptual reviews that the performance of different measures of PNC strongly depends on the assumptions of a certain model of niche evolution (e.g. Revell, Harmon & Collar 2008; Ackerly 2009; Cooper, Jetz & Freckleton 2010). However, in applied studies PNC is still measured with one or the other approach without adequately testing for the underlying evolutionary process (e.g. Buckley et al. 2010), questionable approaches are still frequently applied (e.g. methods relying on taxonomy only, Olalla-Taraga et al. 2011) and general conclusions on the prevalence of PNC in nature rely on these biased studies (Wiens et al. 2010). We thus think it is worth building on earlier conceptual work to point out the importance of assumptions and exemplarily demonstrate the frequency, magnitude and consequences of biases resulting from wrong assumptions. This paper re-visits the different approaches for measuring PNC, demonstrates with simulated data what can go wrong when ignoring the underlying assumptions and exemplifies with own data and literature examples that assumptions are frequently not met.

Methods

We applied the different measures of PNC both to virtual data that were simulated under different niche evolution models and to empirical data on body mass in 17 clades of mammals. In the simulation model we simplify the niche evolution process by assuming that species' niches can be represented by a single abstract trait capturing those optimal environmental conditions in which a species can thrive (hereafter 'niche value'). This niche value evolves according to an Ornstein-Uhlenbeck process along simulated phylogenies.

Simulating niche evolution

In a first step, we simulated a phylogenetic tree under a Yule model (R function birthdeath.tree in package geiger, Harmon *et al.* 2008). In each simulation, a tree with 100 tips was simulated with a branching rate of 0.05 lineages per time unit.

In a second step, we simulated niche values along these phylogenies following an OU-model, where the evolution of the niche value (x) is governed by the following differential equation: $x(t+dt) = x(t) + \alpha(\theta(t)-x(t)).dt + \sigma.dt.\varepsilon$ (Box 2). In this equation, $\varepsilon \sim N(0, 1)$, σ is the Brownian motion rate, θ the optimal value (that can depend on time), α the selection strength, and dt is an elementary unit of time. Niche evolution was simulated not for entire branches at once but consecutively through a discretized continuous time

process (R function evolve.trait in package picante on R-forge, www.r-forge.r-project.org, note that we redefined α in this function such that a value of zero describes BM and 1 describes strong selection towards niche optima). In each simulation, niche evolution always started from a root value of zero and σ was set to 0.01.

Across simulations we varied the strength of selection towards optima, α, the number of optima and the values of optima in order to describe contrasting processes of niche evolution:

1. OU-model with a single optimum (OU1)– In our first set of simulations all nodes and tips in the tree shared the same optimum, which was set to zero while the selection strength, α, varied between simulations. If all species share one optimum and this optimum is equal or very similar to the common ancestor's niche (root niche value), species tend to retain their ancestral niches. We thus suggest that this niche evolution model can be interpreted as increasingly strong PNC for increasing α (for α equal to zero it is a Brownian motion model). As the selective constraint that is exerted onto related taxa is external it could, for example, be interpreted as an environmental selective constraint (Harvey & Pagel 1991; Desdevises *et al.* 2003; Losos 2008).

2. *OU-model with multiple internal optima* (OU_{int})– In our second set of simulations we set the optima of nodes in the OU-model to the niche values of the respective ancestor nodes. Due to these conserved ancestor's trait values we suggest that increasing strength of α can be interpreted as increasing strength of PNC under internal constraints, e.g. due to limits to adaptive evolution (Holt 1996; Gomulkiewicz & Houle 2009), or to a lack of genetic variability (Bradshaw 1991).

3. *OU-model with multiple external optima* (OU_{mult})– In our final set of simulations different clades differ in their external selective optima and these optima also differ strongly from the root value. In these simulations niches diversify quickly over a long time during early evolution and stay more constant during the late period (see also the 'time-dependent stochastic peak shift' model, Revell et al. 2008). When considering the entire phylogeny at once, niches may be interpreted as being labile because they change more extremely than under neutral drift and PNC. However, when considering different parts of the phylogeny separately one may argue that a long period of labile niches is followed by a short period of conserved niches.

To implement this model we needed to simulate niche value evolution towards clades with different environmental optima. To calculate the optima for all nodes of the tree we first identified the tips belonging to the same optima-clade by cutting the phylogenetic tree at a certain time (we chose times that resulted in η different clades with η=10 when not reported otherwise). All species in each clade were assigned the same optimum. The optima were randomly chosen from a set of η values evenly distributed around zero and between the boundary values -β and β. Starting from the optima values of the tips we then calculated the optima for the nodes backwards in time along the phylogeny such that each node's optimum was the mean of the descendants' optima. We chose

Box 2: Ornstein-Uhlenbeck process

Niche evolution can be simulated via an Ornstein Uhlenbeck (OU) process. The OU processes is the simplest mathematical model for an evolutionary process with selection. It is consistent with a range of evolutionary interpretations and varying the parameters results in a variety of distributions consistent with phenotypic evolution under both drift and selection (Butler & King 2004). The OU process models the evolution of a continuous niche value as the weighted sum of a Brownian motion (BM) component and a selection term mimicking stabilizing selection. BM simulates a continuous-time random walk of the niche values along the branches of the phylogenetic tree (Felsenstein 1973). Thus, under BM, the expected variance between ancestor niche values and descendent niche values increases linearly with branch length and is not constrained by additional factors. The selection component describes constraints on niche evolution due to stabilizing selection towards one or several clade-specific optimal values. When selective optima are changing across the phylogenetic tree, the model will mimic niche diversification while one single optimum fixed across the entire tree mimicks niche conservatism (Cooper, Jetz & Freckleton 2010; Kozak & Wiens 2010). When the selection strength is zero, the simulated process equals a Brownian (neutral-like) niche evolution. Thus the basic OU process allows us to simulate a range of different evolutionary scenarios, while changing parameter values and combinations.

this approach to obtain gradually changing optima over time while at the same time allowing for large differences in optima between neighboring clades (as optima were assigned randomly to clades). This is a numeric method for parameterizing the external optima. For the sake of simplicity we did not implement a sub-model simulating emerging environmental niche optima over time. Under relatively large values of β (we used 1 and thus a range of -1 to 1 for the optima if not stated otherwise) niches were increasingly labile under increasing strength of α.

Each simulation scenario in the three sets of simulation was repeated 100 times. Results are presented as boxplots such that the degree of variation among these 100 repetitions is visualized. The number of repetitions was sufficient to differentiate between scenarios but one should note that for smaller trees a higher number of repetitions may be required.

Evolution of body mass in mammals

To complement our simulations, we also studied the evolution of body mass in 17 clades of mammals. These clades were chosen in order to have information on both body mass and phylogeny for at least 20 species, and more than 75% of species described by taxonomists in each clade. Phylogenetic trees for clades came from the supertree of Fritz et al. (2009), except for clades of carnivores and primates (Arnold et al. 2010), Dasyuromorphia and Heteromyidae (Pigot et al. 2012). Adult body masses were extracted from the PanTHERIA database (Jones et al. 2009) and were log-transformed prior to analysis.

Approaches to estimate phylogenetic niche conservatism

1. Phylogenetic signal – We measured phylogenetic signal using Blomberg's *K* (Blomberg, Garland & Ives 2003). Values close to zero indicate phylogenetic independence and values of one indicate that species' niches co-vary in direct proportion to their shared evolutionary history as expected under BM. Higher values indicate stronger phylogenetic signal. We chose Blomberg's *K* as it can take values much beyond those expected under BM (in contrast to Pagel's λ, Pagel 1999) and is especially suitable for simulation models where scenarios can be repeated (Münkemüller *et al.* 2012).

2. Evolutionary rate – We estimated the rate of evolution using the variance of phylogenetic independent contrasts, which assumes a BM model of evolution (Felsenstein 1985b; Cooper, Freckleton & Jetz 2011).

3. Niche retention – We estimated niche retention with Pagel's δ (Pagel 1999), a transformation of branch lengths that contracts or stretches branches depending on their age.

4. Estimation of the α parameter in an OU1 model – We used the *motmot* package (Thomas & Freckleton 2012) to fit the OU1 model. Parameters were estimated by maximum-likelihood, using the independent contrasts algorithm (Felsenstein 1985).

5. Model comparison– In a first step, we applied the common approach and compared the fit of white noise, BM and OU1 on the data (Cooper et al. 2010). For clades of mammals, we also fitted OU models with multiple optima without any *a priori* on the nodes where shifts between selective regimes would occur (Ingram & Mahler 2013). All models were fitted using the SURFACE package (Ingram & Mahler 2013) and compared using AIC (Akaike 1974). Maximum likelihood estimates of model parameters were obtained using large-scale bound-constrained optimization (Byrd et al. 1995), with the maximum number of iterations set to 100,000.

Results

1. Phylogenetic signal – As expected, simulations of a Brownian motion process (Fig. 1a, no selection, α = 0) resulted in a phylogenetic signal of one. Increasing the strength of PNC, i.e. increasing selection strength in the 1-optimum OU-model and the multiple internal optima OU-model, let to decreasing phylogenetic signal.

In contrast, increasing selection strength in the multiple external optima OU-model, i.e. when a long period of labile niches is followed by a short period of niche conservatism, let to an increase of phylogenetic signal to values well above one (Fig. 1a). However, this was only the case for low numbers of optima that were sufficiently different (see Fig. 1b for varying number and range of optima in the multiple external optima OU-model). In summary, if processes different from Brownian motion generated data, phylogenetic signal can be low under phylogenetic niche conservatism and high when niches are more labile.

2. & 3. Evolutionary rate and niche retention – Increasing the strength of PNC, i.e. increasing selection strength in the 1-optimum OU-model and the multiple internal optima OU-model, resulted in decreasing overall estimated rates of niche evolution (Fig. 2a).

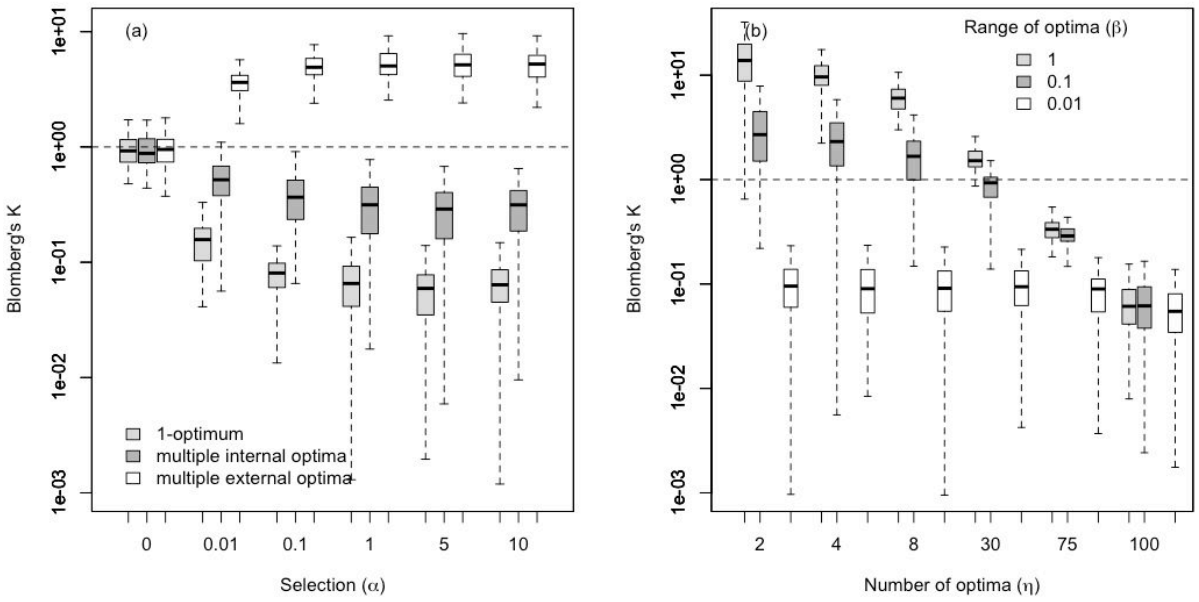

Figure 1: Phylogenetic signal (Blomberg's K) in the simulated data in dependency on the strength of stabilizing selection (α) towards optimal niche values in the three different OU-models (plot a, β=1 here), and on the number of different optima (η) and the range of these optima (β) in a multiple external optima OU-model (plot b, α=1 here). Each boxplot represents 100 repetitions. Note that y-axes are logarithmic and that outliers were not printed.

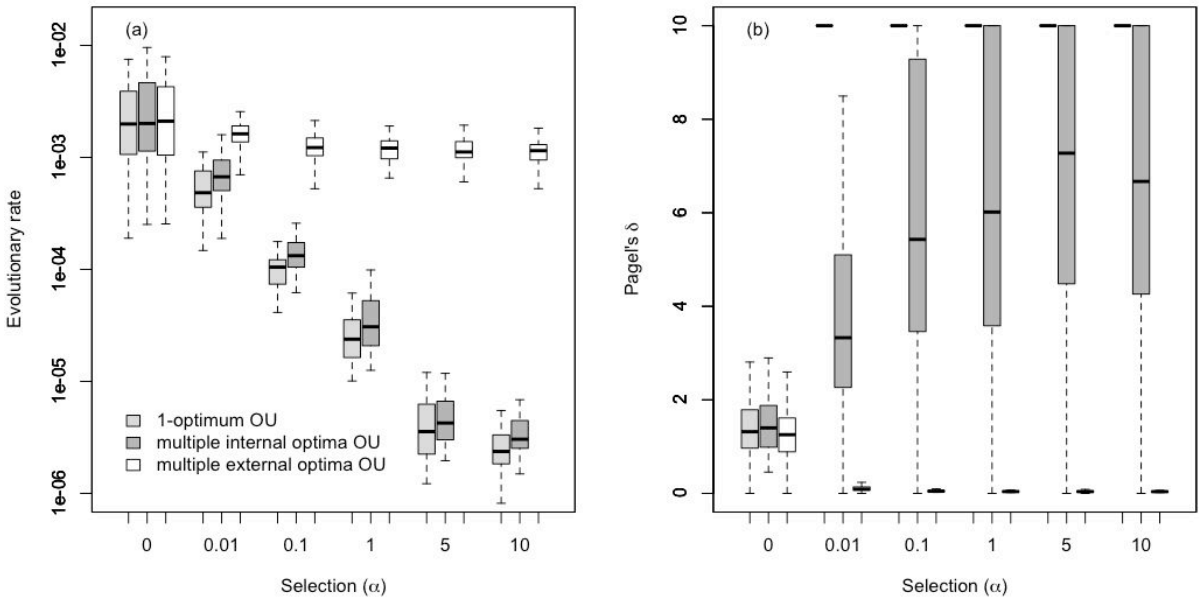

Figure 2: Estimated evolutionary rates (plot a), and Pagel's δ (plot b) in the simulated data in dependency on the strength of stabilizing selection (α) in the three different OU-models. Each boxplot represents 100 repetitions. Note that outliers were not printed and that the y-axis in plot a is logarithmic.

Pagel's δ suggested increasingly more labile niche evolution towards the tips of the phylogeny especially in the 1-optimum OU-model (Fig. 2b). In contrast, in the multiple external optima OU-model, estimated evolutionary rates did not respond to changes in selection strength (Fig. 2a). However, Pagel's δ indicated quickly changing niches towards the root and niche conservatism towards the tips of the phylogeny (Fig. 2b). Obviously, if processes different from Brownian motion generated data but evolutionary rates were estimated based on a Brownian motion assumption, then these estimates are wrong and cannot be easily interpreted. For example, in the 1-optimum OU-model reduced estimated evolutionary rates could be interpreted as indications of phylogenetic niche conservatism but the high values of Pagel's δ would suggest labile niches at the same time. For the multiple external optima OU-model it is the other way around, low values of Pagel's δ indicate PNC while the estimated overall evolutionary rates are not different from Brownian motion expectations.

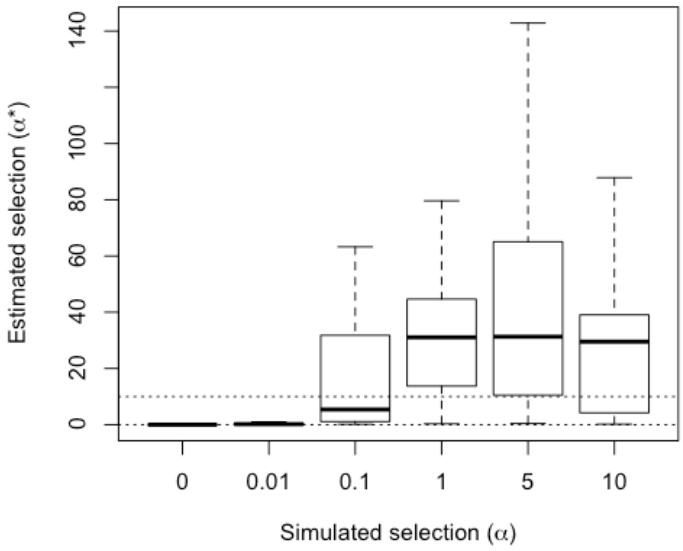

Figure 3: Estimated selection parameter (α*) assuming an OU1 model against the simulated strength of stabilizing selection (α) in data that were simulated with an OU1 model. Each boxplot represents 100 repetitions. Note that outliers were not printed.

4. Estimation of the α parameter – Fitting an OU1 model to data simulated with an OU1 model resulted in extreme overestimations of the strength of stabilizing selection (α, Figure 3).

Fitting OU-models to the different clades of the mammal phylogeny and examples from the literature demonstrate that high estimates of selection strength are frequent (Table 1). This result from the simulated data was supported by the analyses of the mammal clades. Four out of 17 clades had α* higher than 1 and the maximal estimated α* was 72 (Fig. 4).

between 2 and 9 different optima (with the proportion of shifts ranging from 7-17%). The estimated strength of selection (α*) was strong and positively correlated with the evolutionary rate, σ, indicating that these two parameters are difficult to estimate independently. As shown by our simulations (Fig. 1a), α was negatively correlated with phylogenetic signal, K, while σ and K were strongly negatively related (Fig. 4). Thus, high α* values indicate PNC for the same clades for which low K and high α values indicate labile niches. The number of optima was not related to one of the other estimates.

5. Model comparison – The model comparison analyses of the small mammal data revealed that simple Brownian motion or white-noise models were never the best description of the niche evolution processes. The selected multiple-optima OU-models included between 2 and 18 shifts of optima and

In the model comparison analyses of the simulated data a simulated Brownian motion process was in about 95% of the cases rightly identified (Fig. 5, for α = 0). However, a simulated 1-optimum OU process could almost never be distinguished from white noise. This was true already for very weak selection (α

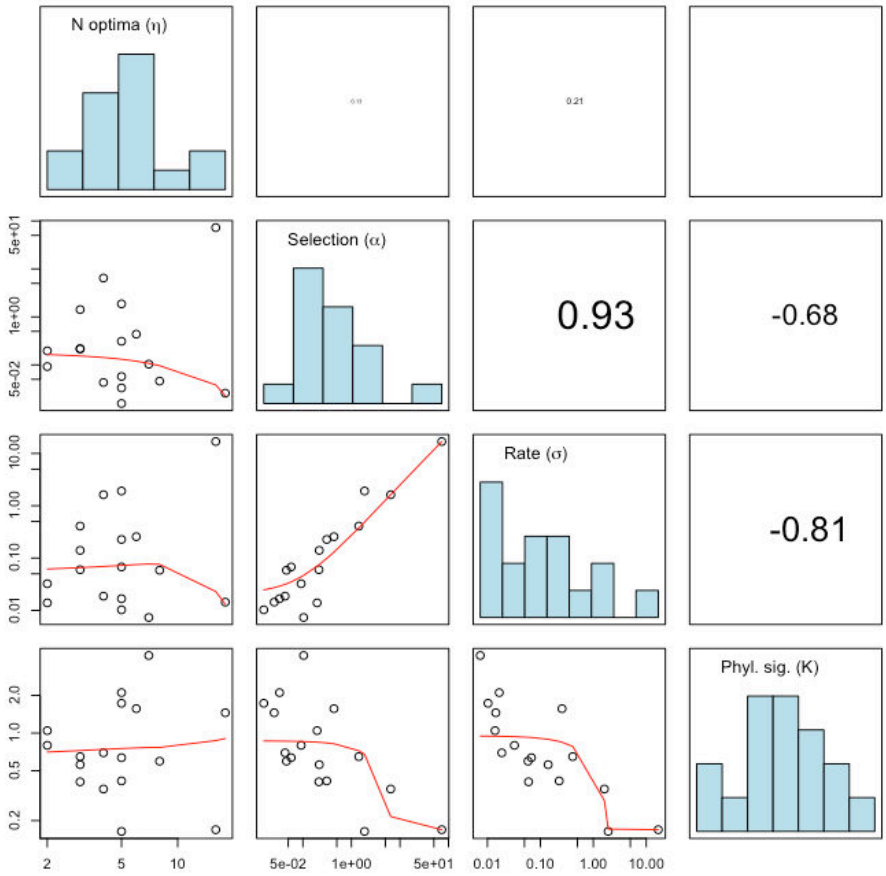

Figure 4: Comparison of estimated parameters during the model selection analysis (and phylogenetic signal, Blomberg's K in addition) for the small mammal data. We considered white noise, Brownian motion and flexible OU-models (shown are selection strength and evolutionary rate for the model with the lowest AIC).

>0.01). A simulated multiple external optima OU-process was almost always misidentified as a Brownian motion process and a simulated multiple internal optima OU-process was identified either as white noise or as a 1-optima OU process (and a few times as Brownian motion for weak selection strength).

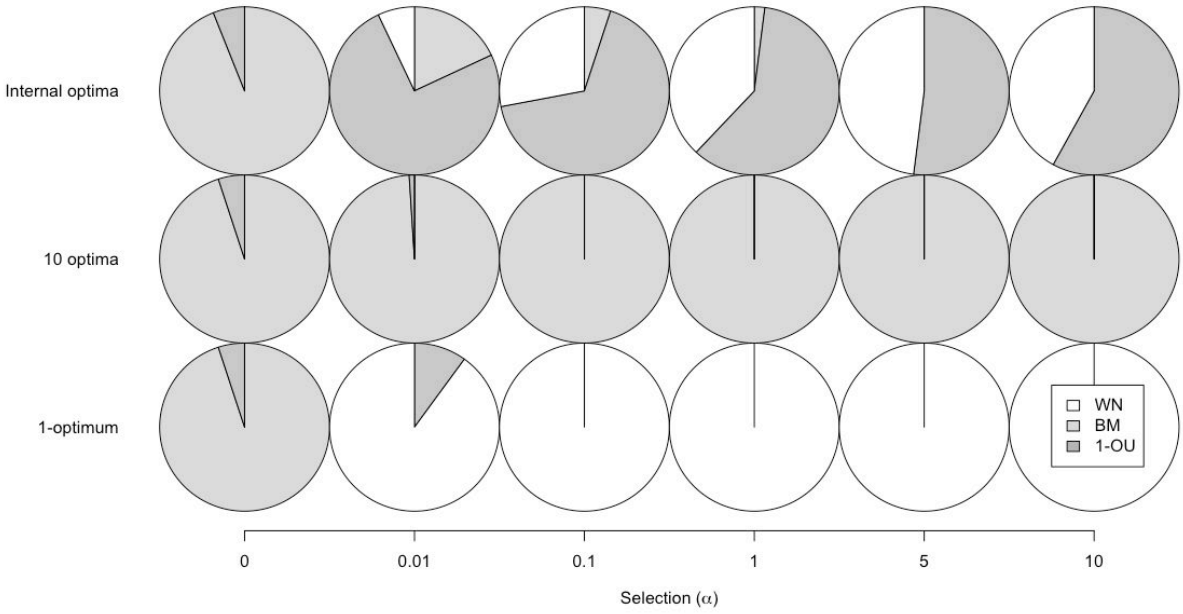

Figure 5: Results of the model selection analysis including white noise, BM and OU1 models for the simulated data in function on the strength of stabilizing selection (α) and the three OU-models. Pie charts indicate how often which model was chosen in the 100 repetitions.

Discussion

Assumptions are an integral part of statistical methods. It is well established that the performance of estimates and tests of PNC depends on the model of niche evolution. Nevertheless, PNC approaches are often applied without knowing which model of niche evolution underlies the data. Two arguments could support this practice. First, the often-assumed simple models, such as Brownian motion, could well represent the vast majority of studied cases of niche evolution. Second, PNC approaches could be robust to moderate violations of model assumptions. Our study demonstrates that both of these arguments fail in practice. In our field data and in examples from the literature the assumption of a simple niche evolution model was often wrong. Analyzing our simulated data with approaches assuming 'wrong' niche evolution models frequently led to strong biases and wrong conclusions. These findings highlight the need to test assumptions of PNC approaches before applying them as these assumptions are frequently violated and violations easily lead to wrong conclusions.

BM is not always a good null model

In the 17 empirical examples that we studied, we found that BM was never the model best describing niche evolution. Other studies that compared alternative models have found higher evidence for BM but shown that it is often not the best model (Harmon et al. 2010). Given that BM is central to several tests of PNC, like phylogenetic signal or evolutionary rates, it seems crucial that empirical studies first test whether this model appropriately fits the data or not. Importantly, model comparisons should not be limited to the BM/white noise/OU trilogy (Cooper et al. 2010, Wiens et al. 2010) because in this case complex scenarios of niche evolution could be erroneously identified as BM (see Figure 5). Instead, highly flexible models where different processes are allowed to act in different parts of the trees (*e.g.* OU models with multiple optima) should be routinely included.

Measures of PNC based on BM go wrong when assumptions are not fulfilled

Phylogenetic signal remains frequently used for measuring PNC in empirical studies. However, several lines of evidence indicate that phylogenetic signal does not measure PNC. Revell et al. (2008) already showed that stabilizing selection (one of the major processes causing PNC) can lead to low phylogenetic signal. In addition, we have shown here that multiple processes, including some processes simulating very labile niches, can produce similar patterns of high phylogenetic signal (Fig. 1). This shows that, contrary to a common conception in the empirical literature, phylogenetic signal is completely unrelated to PNC.

Evolutionary rates are a useful means of comparing the *relative* speed of niche evolution (and thus the strength of PNC) in different clades if BM is the right evolutionary model (Cooper et al. 2010). Models where different clades are allowed to have different evolutionary rates (O'Meara et al. 2006) thus seem appropriate when the question is the *relative* strength of PNC between clades. However, our simulations show that evolutionary rates can be highly misleading when the wrong model is assumed. Indeed, under an OU process which is constant over time and in different parts of the tree, evolutionary rates measured using BM are wrongly estimated. This is because the OU process has a finite stationary variance, which is $\sigma^2/2\alpha$. The variance of niches under an OU process thus tends to be reduced when the selection strength increases but is constant over time, which causes estimates of evolutionary rates obtained under a BM model to decrease when the selection strength increases (Figure 2A) or when the age of the clade increases (see Fig. 3 in Harmon et al. 2010). If this limitation is fully acknowledged and understood, evolutionary rates measured using BM could however be used to measure the 'average rate of evolution' in a clade whatever the true model of evolution. This could be interesting for comparing multiple groups with no desire to identify the true process of niche evolution.

The niche retention parameter, δ (Pagel 1999), is meant to measure whether most niche variance accumulated early or late in the history of a clade. Our

simulations show that when niches do not evolve under BM this parameter can also lead to wrong conclusions. In particular, under an OU model with one single optimum, δ indicates that most variance accumulated close to the tips of the phylogeny (Figure 2B). This is statistically true but should not be interpreted as evidence that niche evolution has accelerated recently, because in this case the OU process has remained constant through time.

Caution when interpreting the strength of attraction towards the optimum in an OU model

Interpreting the estimated value of the α parameter in an OU model with one or multiple optima is appealing because this should in theory be related to the strength of constraints on niche evolution. However, our simulations show that this parameter is difficult to accurately estimate, especially for high values (Figure 3). In fact, the stationary variance of the OU process appears to be much more accurately estimated (data not shown). This measure quantifies the relative strength of drift vs. that of selection, and should rather be the quantity that is interpreted in empirical studies.

Furthermore, even for moderate values of α in an OU model with one optimum, AIC would favor a white noise model because it produces relatively similar patterns (*i.e.* niche distances poorly correlated to phylogenetic distances) and has fewer parameters (Figure 5). This is particularly problematic since white noise is often interpreted as a model of lability while OU with one optimum is used to model PNC (Cooper et al. 2010, Wiens et al. 2010).

Interpreting the results of highly flexible models

Our investigation of the evolution of body mass in 17 groups of mammals revealed that flexible models that include different selective regimes in different parts of the tree often are the ones best describing the data. Although these models have a high number of parameters, they are nonetheless frequently selected using AIC. As larger and larger phylogenies are published, these models will most probably take an increasing importance in the study of PNC (O'Meara 2012). OU models with multiple optima are particularly interesting representations of the macroevolutionary adaptive landscape, the analogue of Wright's adaptive landscape over long periods of time (Simpson 1953). In this landscape, each different optimum of the OU model is an adaptive peak, which width is determined by the stationary variance of the OU process, $\sigma^2/2\alpha$. Strict PNC in this landscape might be evidenced when only one peak is occupied by a clade. However, when comparing the number of different peaks, the number of transitions between them and the width of peaks in different clades, the *relative* importance of PNC can be assessed. Some clades might indeed shift from one peak to the other more often than others indicating greater niche lability, while some may have narrower peaks, which would indicate stronger PNC.

Conclusion

Although part of the problems that we highlight in this paper have already been published (*e.g.* Revell et al. 2008, Cooper et al. 2010), they have not been considered in most applied studies. We hope that our review helps to highlight and illustrate some of the most common problems and contributes to a better common practice. The main message of this article is that many alternative models of niche evolution should be compared when analyzing niche evolution. Depending on the model that best fits the data, different methods should be used to measure the strength of PNC. Among the most promising tools for investigating PNC, highly flexible OU models (Beaulieu et al. 2012, Ingram & Mahler 2013) enable characterizing the macroevolutionary adaptive landscape (Simpson 1953) in which species' niches have evolved. In analyzing such landscapes, the number of shifts between different peaks as well as the width of peaks will help characterizing the degree of PNC.

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ARTICLE 1.2

INFLUENCE DE PROCESSUS BIOGEOGRAPHIQUES NEUTRES SUR L'EVOLUTION DES NICHES CLIMATIQUES

NEUTRAL BIOGEOGRAPHY AND THE EVOLUTION OF CLIMATIC NICHES

Florian C. Boucher, **Wilfried Thuiller, T. Jonathan Davies & Sébastien Lavergne**

ABSTRACT

Recent debate on whether climatic niches are conserved over macroevolutionary timescales has focused on how phylogenetic niche conservatism can be measured by deviations from a Brownian motion model of evolutionary change. However, to date, there has been no explicit evaluation of this methodological approach. In particular, the fact that climatic niches are usually obtained from distribution data and are thus heavily influenced by biogeographic factors has largely been overlooked. Our main objective here was to test whether observed patterns of climatic niche evolution on phylogenetic trees might arise from neutral dynamics rather than complex adaptive scenarios and niche conservatism. We develop a model inspired by Neutral Biodiversity Theory, where individuals randomly migrate and undergo speciation independently of climate and where distributions result primarily from dispersal and competition for space, independent from climate. We then sample the climatic niches of each species according to its geographic position and evaluate their macroevolutionary patterns. We show that neutral biogeographic processes produce outcomes strongly differing from Brownian motion, and that the neutral expectation for the evolution of climatic niches is better captured by a model of punctuated evolution with constraints due to landscape boundaries. We suggest that deviation from Brownian motion alone should not therefore be used as evidence for phylogenetic niche conservatism.

Keywords: comparative analysis; neutral biodiversity theory; phylogenetic niche conservatism; Ornstein-Uhlenbeck process; punctuated equilibrium

INTRODUCTION

Phylogenetic niche conservatism (PNC), the tendency for species and clades to retain ancestral niche attributes across large temporal scales, is a surprisingly controversial issue (Losos 2008; Wiens et al. 2010). In particular, the evolution of species' climatic niches has implications for understanding a wide range of questions in evolutionary biology, including the origin of broad-scale diversity patterns (Buckley et al. 2010), the drivers of speciation (Kozak et al. 2008), invasive species niche shifts (Petitpierre et al. 2012) and the response of species and communities to climate change (Lavergne et al. 2010). Despite intensive research during the last decades, the conditions that have triggered or impeded climatic niche evolution remain hotly debated, with a major disagreement on how observed macroevolutionary patterns of species niches should be compared to neutral expectations (Losos 2008; Wiens et al. 2010).

Most common approaches aimed at investigating PNC share several basic premises and assumptions. Climatic niches are often measured as species' mean position over continuous environmental gradients (e.g. Hof et al. 2010; Pyron and Burbrink 2012). This choice is usually made because it enables climatic niches to be characterized in a broad sense without the practical difficulty to obtain physiological estimates of climatic tolerance for a large number of species (but see Kellermann et al. 2012). However, climatic niches measured this way are emergent properties at the species level (Vrba and Gould 1986), a product of the interaction between individual physiology and extrinsic factors including biotic interactions and dispersal limitation (Soberón 2007). This interaction has lead some authors to argue that climatic niches do not evolve by descent with modification and thus should not be analyzed in a phylogenetic context (Grandcolas et al. 2011). The strength of PNC is then usually assessed by comparison to a Brownian motion (BM) model of evolution as the neutral expectation. Under BM, traits are inherited from a common ancestor but diverge gradually over time independently according to a continuous random walk. BM is used to mimic genetic drift or selection in a variable environment (Edwards and Cavalli-Sforza 1964; Felsenstein 1985). Different approaches to the study of PNC examine different deviations from BM: (i) phylogenetic signal measures the tendency for closely related species to resemble each other more or less than expected under BM and (ii) model comparisons that contrast the fit of the BM model to alternative models, evaluate evidence for selective constraints on niche evolution (Wiens et al. 2010). Here we question the underlying assumption that BM provides an appropriate neutral expectation for climatic niches.

To our knowledge, there has been no rigorous assessment of the major assumptions underlying tests of PNC outlined above. Here, we attempt a first step towards bridging this gap, and evaluate whether in the absence of any climate-induced processes, wrong conclusions can be made concerning PNC when assuming a neutral BM model. In particular, we test whether observed patterns of punctuationism or constraints on climatic niche evolution could result from neutral dynamics that are independent of climate. We use models of neutral biogeography that explicitly include the processes of speciation and migration to free us from assumptions of BM. Spatially explicit simulations of the neutral biodiversity theory (NBT, Hubbell 2001) are well suited for this purpose. Specifically, NBT assumes performance equivalence between individuals in terms of speciation, migration and competitive ability regardless of species identity. NBT also models ecological drift via a simple limitation of the carrying capacity of local communities. For these reasons, NBT provides a useful link between biogeographic and ecological processes, as illustrated in macroevolutionary studies of range size heritability (Mouillot and Gaston 2007) and phylogenetic tree shape (Davies et al. 2011).

In this article, we confront the traditional neutral model in macroevolution (BM) with an alternative neutral biogeographic model (NBT) of climatic niche evolution. Specifically, using an absurdum argument where our simulated climatic niches do not result from adaptive process but rather from purely neutral spatial dynamics, we ask the following questions: (1) are phylogenies informative for studying climatic niche evolution, i.e. do climatic niches exhibit phylogenetic signal when they arise via neutral spatial dynamics? (2) is gradualism a reasonable neutral expectation for the evolution of

climatic niches on geological timescales? and (3) can constraints on climatic niche diversification arise simply through bounded geographic space?

To address these questions we simulate clades evolving under different NBT models in which dynamics are independent from climate. We first examine whether such models generate macroevolutionary patterns resembling those produced by BM, i.e. strong phylogenetic signal and gradualism. We then compare the fit of NBT models to alternative macroevolutionary models (i.e. stabilizing selection and punctuated evolution) to describe more in detail the process of niche evolution expected from a neutral biogeographic scenario of species diversification and range dynamics. Finally, we show that assuming an incorrect model of niche evolution, and in particular wrongly assuming BM, can lead to spurious conclusions in analyses of trait-climate relationships.

MODEL PRESENTATION

Death, migration and reproduction

To simulate the evolution of a clade in geographic space, we developed a model that includes the processes of speciation and migration, derived from NBT. We modeled clade diversification in a 'continent' represented as a rectangular lattice with hard boundaries. The continent was 51x21 pixels and thus stretched more in latitude than in longitude. Each pixel in the lattice had a finite carrying capacity set to 20 individuals, leading to competition for space and hence ecological drift. Simulations were initiated with an empty lattice except for the central pixel, which was at carrying capacity with individuals of the ancestral species. Simulations then followed Davies et al. (2011): at each time step an individual was randomly chosen in the landscape, it either speciated with probability *b* (per-capita speciation rate, see below for speciation modes) or died and was replaced by the offspring of another individual. This new individual, irrespective of species identity, could either be from the same pixel or from the eight-neighboring pixels with probability *m* (migration rate). Because we did not assume all pixels were at carrying capacity at the beginning of the simulations, we thus created a reproductive advantage for individuals in close proximity to empty slots. Simulations were terminated after 10^8 individual replacements, which roughly corresponded to 4,500 generations. Metacommunities were then recorded (Fig. 1) and phylogenetic trees for extant species were reconstructed using the recorded history of speciation events.

Speciation

We modeled two different modes of speciation, both sharing the basic assumption that more abundant species have a greater chance to speciate (Hubbell 2001). For the sake of simplicity and computational tractability, speciation occurred instantaneously in our simulations.

1) We first modeled a modified version of point mutation speciation (Hubbell 2001): when a randomly chosen individual within a pixel underwent speciation, a random fraction of conspecifics occurring in the same pixel were delineated as the new species (following Davies et al. 2011). In this version of point mutation one of the two daughter species has low abundance and occupies only one location, that can be anywhere in the ancestral range. Speciation via polyploidization (Abbott et al. 2013) is probably the mode of speciation that is best embodied by point mutation.

2) Despite the recent accommodation of more realistic models of speciation (e.g. Desjardins-Proulx and Gravel 2012; Rosindell et al. 2010), NBT still lacks an explicit treatment of vicariance. To overcome this limitation and to keep the simulation model tractable, we proposed an alternative speciation mode that is based on the vicariance model developed by Pigot et al. (2010, see also Davies et al. 2005). In this model, a geographic barrier is assumed to bisect the species range, splitting the target species into two. To match the philosophy of previous spatial NBT models, we specified that the geographical barrier would run through the local pixel where an individual had been randomly selected to undergo speciation. The orientation of the barrier was then randomly chosen and only the species of the

selected individual was subdivided. We chose this strategy because it better captures the contingency of speciation events where barriers are more or less permeable to different species and are rarely constant trough time (e.g. Lavergne et al. 2012).

Species' climatic niches

We first modeled a single climatic variable as a function of latitude, so that within each pixel climate was given by latitude+ε, where ε is a random normal deviate (σ^2=2, and latitude ranges from -25 to +25). Although this latitudinal dependence is rather strong, it was meant to broadly mirror the distribution of temperatures at continental scale. In a second step, we used mean annual temperature maps from six mountainous regions of the World. This provided examples of landscapes that match reality and include both a latitudinal dependency and a strong spatial aggregation of climate. Climate had no impact on the simulations (i.e. it did not influence individual performance) but at the end of each run the climatic niche of each species was calculated as the mean climate over the pixels where the species was present, as usually done from atlas data in comparative analyses (e.g. Barnagaud et al. 2012; Hof et al. 2010; Pyron and Burbrink 2012).

Our simulations model the evolution of species ranges via migration and biotic interaction (included in the

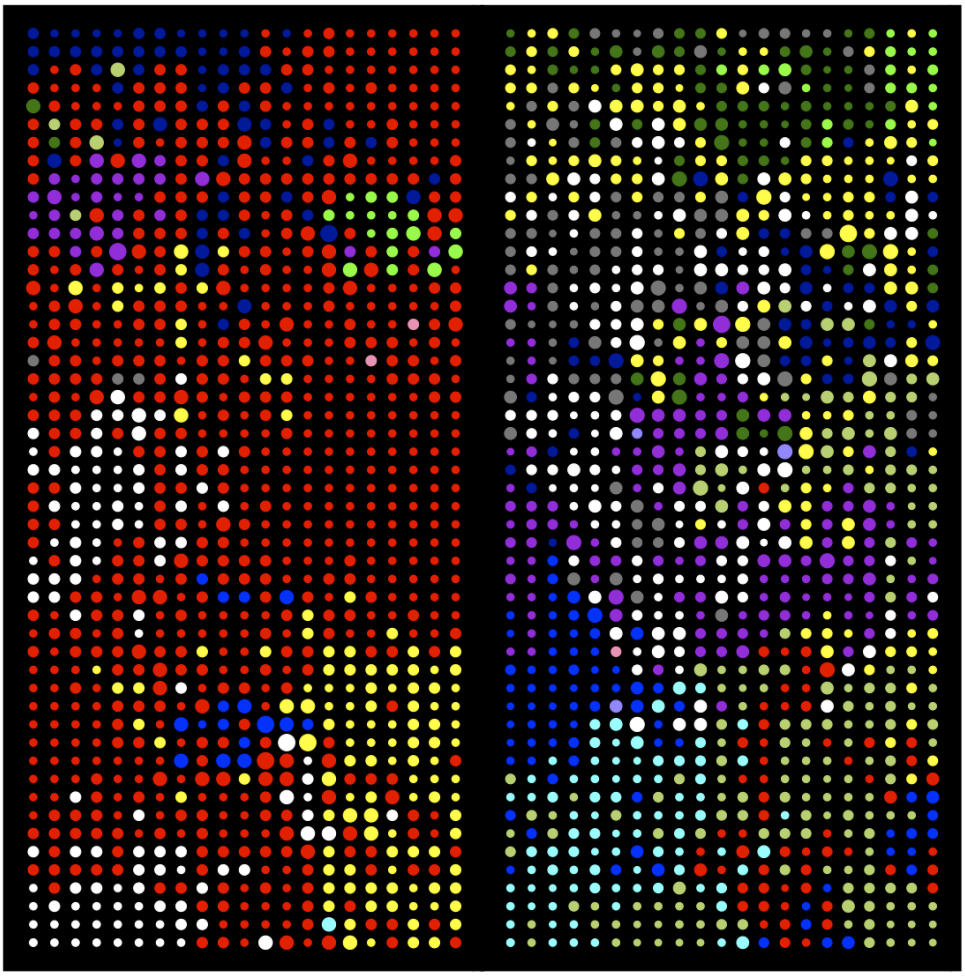

Figure 1. Snapshots of two meta-communities after 4,500 generations. Each local community is represented by a filled circle colored according to the most abundant species, and which size is proportional to local species richness. Left panel: simulation under point mutation speciation, with m=0.07 and b=1.3^{e}-5 (16 species). A few species are very abundant, while all others are rare. Right panel: simulation under the vicariance model, with m=0.13 and b=4.1^{e}-7 (14 species). Abundances are more even between species.

model as carrying capacity), and provide a dynamic neutral model of species climatic niches. Under such a scenario, actual niche changes may be small, and thus do not call for the evolution of physiological tolerances, or require assumptions regarding individual performance differences across the underlying climatic gradient We suggest that our simulations might match to a scenario in which fundamental niches are generally broad, encompassing all climates found in the landscape and thus provide a useful neutral model for the evolution of climatic niches. In this framework, the term evolution is used in a weak sense, since change in the climatic niche is a product of migration, speciation and ecological drift.

Parameter choice

To generate robust estimates of the relative importance of speciation mode, migration rate and per-capita speciation rate, we performed 2500 simulations for each speciation mode. Because simulations were uninformative when only one species was present at the end of the run, we retained only simulations with final species richness >1, generating 1402 replicates for point mutation and 2210 replicates for vicariance. For computational tractability, values of speciation rate were selected following preliminary analyses so as to produce trees with less than 1000 species. Speciation rate was typically an order of magnitude higher in point mutation (values continuously varying between $2e^{-6}$ and $2e^{-4}$ speciation events/individual) than in the vicariance scenario ($2e^{-7}$-$2e^{-5}$) due to higher chance of extinction by ecological drift. For both speciation modes, we varied migration rates uniformly between 0 and 1.

In the simulations we present, the maximum number of individuals in the landscape was 21,420, and the number of generations over which the history of the clade was followed was less than 5,000. As in all such models, these parameters are highly unrealistic if they were to be compared with real metacommunity sizes (Ricklefs 2003), or to timescales necessary to complete many speciation events. Indeed, simulations considering more realistic values would require several centuries of processing time and analytical solutions or coalescent techniques have not yet been developed for the modeled speciation modes. We therefore derive analytical expressions for niche evolution in the next section to further explore parameter space and gain a better understanding of model behavior.

Evolution of climatic niches during anagenesis

In our simulations, the evolution of the climatic niche during anagenesis is a succession of two steps: death of an individual and birth of a new individual (with migration). In the absence of boundaries (i.e. before domain boundaries have been reached) it is straightforward to show that the expected value of the niche (after either of these two steps) remains unchanged:

$$E[Niche(t+dt)]=Niche(t) \quad (1).$$

The niche thus follows a succession of random steps with no direction bias. The expected variance of these random steps can be obtained separately for each step:

$$Var_{death}(Niche(t+dt)-Niche(t)) = \frac{1}{K \times L \times l} \times \frac{N(t)}{(N(t)-1)^2} \times Var(y_i(t)) \quad (2)$$

$$Var_{reproduction}(Niche(t+dt)-Niche(t)) = \frac{1}{K \times L \times l} \times \frac{N(t)}{(N(t)+1)^2} \times \left[Var(y_i(t)) + \frac{3}{4} \times m\right] \quad (3)$$

where N(t) is the number of individuals in the focal species at time t with latitudinal positions $y_i(t)$, m is the migration rate and K the carrying capacity in one pixel. L and l are the dimensions of the landscape. The variance of individual positions can be interpreted as the breadth of the species' niche. Therefore, during anagenesis and before the boundaries of the landscape have been reached, the mean niche of a species moves according to a succession of random steps with no trend. This random walk is however different from Brownian motion since its variance is not constant over time but depends on the population size and niche breadth of the species. Importantly, migration is not the only contributor to niche change: large niche breadths and small population sizes also speed up niche evolution.

The above calculations hold only when the species is unbounded; when individuals approach the edge of the

domain, a trend towards the middle of the landscape will appear. Such constraints are of course more important when the migration rate is high since individuals will reach the boundaries of the landscape sooner. Given that in our simulations one generation corresponds to K×L×l individual replacements, 1/(K×L×l) can be interpreted as the basic unit of time *dt*. Hence, increasing any of these three parameters would not modify model behavior but only increase the number of iterations one has to wait before seeing the effect of landscape boundaries. We are thus confident that the simulations we present cover a sufficiently broad range of scenarios of speciation and migration to be representative of model behavior for more realistic values of K, L and l. Because we could not treat the effects of landscape boundaries and speciation analytically, we explored their effects using comparative analysis.

MACROEVOLUTIONARY ANALYSIS OF SIMULATION OUTCOMES

Comparison to macroevolutionary models

As a first attempt to describe the patterns of niche evolution produced by our simulations, we calculated two indices commonly used in comparative analyses: Pagel's λ and κ parameters (Pagel 1994; Pagel 1999), which quantify departures from BM. First, λ was used to assess phylogenetic signal. It has been shown to be one of the best measures of phylogenetic signal since it can detect deviations from BM under a wide range of evolutionary models (Münkemüller et al. 2012). Pagel's λ is a multiplicative parameter affecting the phylogenetic covariances between the tips of the tree, and equals 1 when signal is equal to that expected under BM. At the other extreme, λ=0 indicates no signal, such that phylogenetic distances between species do not correlate with niche differences. Support for λ=0 in our simulations might indicate (but not demonstrate) that climatic niches are independent from phylogeny (Grandcolas et al. 2011). Second, Pagel's κ was used to measure punctuationism (Gould and Eldredge 1977) in niche evolution. This parameter exponentially stretches or compresses branch lengths of the tree in order to test whether topology is a better predictor of inter-specific niche differences than branch lengths. When κ equals zero evolution is independent from the branch lengths, indicating punctuated evolution. When κ equals unity, a model of gradual evolution is supported, as expected under Brownian motion.

Phylogenetic signal has been widely used in the literature to measure PNC (e.g. Hof et al. 2010; Olalla-Tarraga et al. 2011); however, there is growing evidence

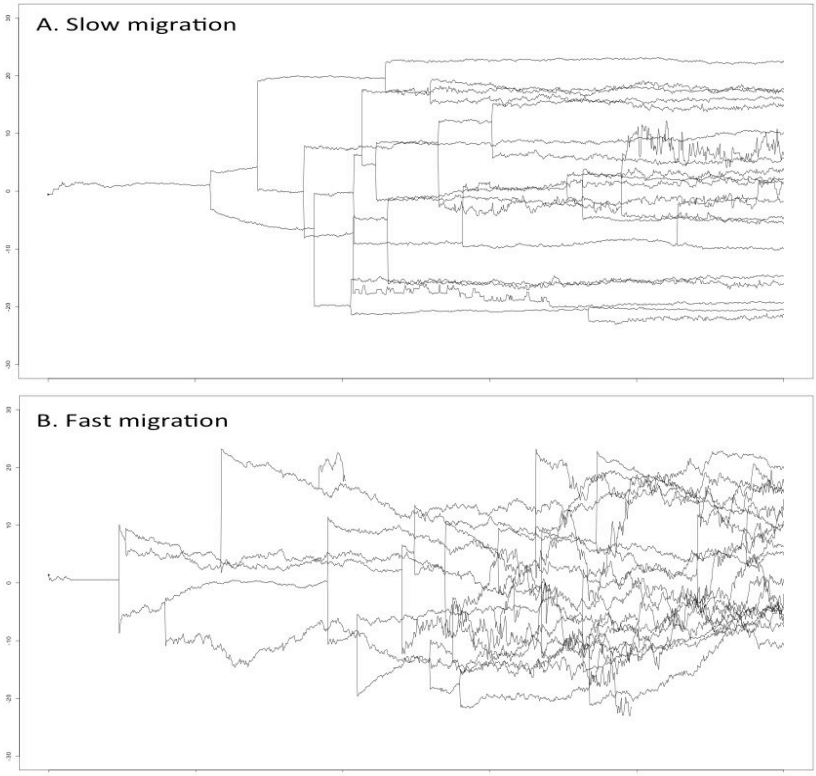

Figure 2. Evolution of the mean climatic niche in the vicariance model. Each traitgram (time on the x-axis, mean climatic niche on the y-axis) illustrates the temporal process of climatic niche evolution during $2.5e^7$ steps in simulations under the vicariance model. A. For low migration rates (here *m*=0.01), almost all evolution happens at speciation. B. For high migration rates (here *m*=0.9), niche shifts also occur at speciation but mean niches tend to be pulled back towards the average climate of the landscape.

that phylogenetic signal *per se* does not give any insight into the underlying processes driving niche evolution (Revell et al. 2008). Therefore, to explore further the process of niche evolution, we compared the fit of alternative macroevolutionary models to our simulated data (Wiens et al. 2010). We evaluated five alternative macroevolutionary models using Akaike's Information Criterion corrected for small sample sizes (AICc): (1) BM; (2) the κ model (KAPPA, Pagel 1994) that adds some degree of punctuationism to BM; (3) an Orstein-Uhlenbeck process (OU, Butler and King 2004) where species are subject to BM but also to selection towards a common optimum; (4) OU with strict punctuationism (OUp) where all branch lengths in the tree are set to unity and finally (5) white noise (WN), a non-phylogenetic model where all niches are drawn from a normal distribution regardless of shared ancestry between species. These macroevolutionary models do not form an exhaustive list but allow us to evaluate three alternative hypotheses. First, support for WN would indicate that phylogenetic relationships do not explain niche differences between species, consistent with extremely fast and recent niche diversification. Second, if KAPPA or OUp have good fit to the data, a model of punctuated evolution would be supported. Third, support for OU or OUp would show constraints on niche evolution.

Potential biases in the analysis of trait-climate relationships

To evaluate the impacts of misspecifying the model of niche evolution, we use additional trait simulations to explore potential biases in studies trying to find biological correlates of climatic niches. First, we verified that OUp is discernable from BM and OU and that parameters (rate of evolution, σ^2 and selection strength, α) were correctly estimated. We then asked how misspecifying the underlying model of climatic niche evolution might effect conclusions regarding correlation estimates. Using the phylogenetic trees obtained from each NBT simulation we (i) simulated the evolution of another niche-related trait (Y) evolving independently from the climatic niche under an OUp model (σ^2=1, $0.05 \leq \alpha \leq 0.9$) and estimated the correlation (Type I error) between this trait and the observed climatic niche from the NBT simulations using phylogenetic generalized least squares (Grafen 1989) assuming the various models of evolution specified above (OUp, BM, OU, KAPPA, WN and Pagel's λ); and (ii) simulated a second niche-related trait as Y=niche+ε, where ε evolved under an OUp model, and here examined Type II error by fitting the same set of comparative models.

All analyzes were run in R (R Development Core Team 2012), using packages *ape* (Paradis et al. 2004), *caper* (http://cran.r-project.org/web/packages/caper/), *geiger* (Harmon et al. 2008) and *phytools* (Revell 2012).

RESULTS

The two modes of speciation yielded slightly different biogeographic patterns (Fig. 1). Under point mutation, many very rare species were produced (on average the least abundant species occupied 1.3 pixels out of 1071 in the landscape), and the resulting phylogenetic trees were highly unbalanced (see Appendix G). In contrast, vicariance produced fewer rare species (the least abundant occupied on average 5.9 pixels) leading to more balanced phylogenetic trees (see Appendix G). However, phylogenetic tree shape did not seem to influence strongly our results: although phylogenetic signal was positively correlated with imbalance, this explained only little variance across simulations (R^2=0.24 for point mutation and R^2=0.09 for vicariance). In nearly all simulations (3603 out of 3612), the metacommunity was at carrying capacity by the end of the simulation, meaning that the boundaries of the landscape had been reached and that each local community was saturated with individuals. The number of extant species ranged between 2 and 952, with mean = 107.8, depending on birth rate and speciation mode.

1. **Patterns of climatic niche evolution**

Simulations yielded values of phylogenetic signal in climatic niche ranging from λ=0 (no signal) to λ=1 (equal to BM expectations), covering the range of values

reported in empirical studies. Both speciation modes showed the same qualitative pattern: phylogenetic signal was moderate for low rates of both birth and migration, generally increasing with birth rate and decreasing with migration rate (Table 1).

Under both modes of speciation, climatic niche evolution tended to be largely punctual (κ_{mean}=0.32±0.16 for point mutation and κ_{mean}=0.23±0.12 for vicariance), suggesting niche stasis along branches of the tree and fast niche evolution during cladogenesis. This pattern is well illustrated by the traitgrams in Fig. 2, which show the shifts in climatic niches at speciation.

	Point mutation	Vicariance
Intercept	0.69 (p<2e-16)	0.87 (p<2e-16)
Migration rate	-0.83 (p<2e-16)	-0.98 (p<2e-16)
Speciation rate	2.16 e3 (p<2e-16)	1.26 e4 (p<2e-16)
Migration*Speciation	548 (p=0.26)	2.64 e4 (p<2e-16)
Number of simulations	1402	2210
Adjusted R-squared	0.49	0.63

Table 1. Dependency of phylogenetic signal on migration and speciation rates. For both speciation modes, we explored the effect of model parameters (migration, speciation rates and their interaction) using a linear model. The number of simulations for each model and the goodness of fit of the model are also reported. Note that values of speciation rate were 10 times smaller for vicariance than for point mutation, which explains the 10-fold differences in the coefficients between the two models. Models with quadratic terms were also fitted, but were rejected due to higher AIC scores.

2. Process of climatic niche evolution

The process of niche evolution did not strongly depend on the mode and rate of speciation but was highly influenced by migration rate. For both speciation modes, Brownian Motion (BM) was often the worst fit model (ΔAICc>11 in comparison with all other models on average over all simulations). Overall, models including some degree of punctuationism had a better fit to the data ($\Delta AICc_{BM\text{-}KAPPA}$=118.4 and $\Delta AICc_{OU\text{-}OUp}$=36.07 on average). KAPPA was the best model for low migration rates (Fig 3), but when migration was higher, constraints on niche evolution were detected and an Ornstein-Uhlenbeck model with strict punctuationism (OUp) had the best fit (Fig. 3, see also Fig. 2B). The strength of selection estimated in the OUp model (α) increased with migration rate (p-val<$2e^{-16}$ for both speciation modes). In simulations where OUp had the best fit, α ranged from $2e^{-9}$ to 1.26 (mean=0.31) for point mutation, and from 0.06 to 0.91 (mean=0.32) for the vicariance model (although these values might be underestimated due to extinction). A non-phylogenetic model (white noise, WN) was sometimes preferred for very low birth rates and high migration (Fig 3), which generally produced trees with less than 10 species.

When using real climatic landscapes from six mountainous regions of the World, results supported even more strongly the OUp model, which appeared to have the best fit even for low migration rates (Fig. B.2).

3. Potential biases in the analysis of trait-climate relationships

Type I error in tests of the correlation between the two niche-related traits (Y and the niche from our simulations) were high (>30%) when either the BM or an OU model was assumed to describe the evolution of the residuals of this relationship (Table 2). In contrast, specifying the true evolutionary model under which residuals evolved, OUp, dramatically reduced Type I errors (Table 2). Transforming the phylogenetic covariances matrix using the maximum likelihood estimate of Pagel's λ also improved Type I errors, but perhaps most surprisingly, even a model of no phylogenetic structure (i.e. WN) was vastly superior to both the BM and OU models. Type II error was very low (0.3%) when using the correct OUp model, whereas for all other evolutionary models, the true correlation between Y and the niche very often remained undetected (Type II error rate >20% for all other models).

	WN	BM	LAMBDA	KAPPA	OU	OUp
Type I error rate	4.8%	46.0%	5.2%	8.4%	30.5%	5.6%
Type II error rate	37.2%	21.4%	30.2%	20.6%	24.8%	0.3%

Table 2. Detection of correlated evolution under the OUp model. Five different macroevolutionary models classically used in comparative analyses were confronted to the OUp model to test a relation between a trait Y and the niche . First, Y was simulated to be independent of the niche values but following an OUp model and type I error rate was assessed by recording the percentage of simulations where a false correlation was detected at the 5% level. Similarly, Type II error rates were estimated as the proportion of existing correlations that remained undetected at the 5% level when Y was simulated to be linearly correlated to niche values assuming an OUp model of evolution for the residuals.

DISCUSSION

Phylogenetically informed comparative analyses are increasingly being used to investigate the evolution of climatic niches, yet there has been little appreciation that common measures such as the mean position of species across a climatic gradient might arise from purely neutral biogeographic processes. The role of biogeography has thus been largely overlooked in the literature on niche evolution and conservatism (but see Freckleton and Jetz 2009). Here, we show that a simple neutral model of biogeography, in which species spread and speciate independently of climate, can generate varying patterns of climatic niche evolution, depending on speciation mode, migration rate and speciation rate. Our analysis reveals several major features of climatic niche evolution relevant for comparative analysis, and the study of PNC. These results caution against the overuse of traditional phylogenetic signal metrics and macroevolutionary tests assuming BM as the neutral expectation to investigate climatic niche evolution.

Migration rate and phylogenetic signal in climatic niches

Phylogenetic signal remains a commonly used measure in macroevolutionary studies of climatic niche evolution (e.g. Hof et al. 2010; Olalla-Tarraga et al. 2011) in spite of recent warnings concerning its interpretation (Revell et al. 2008). In particular, low signal is often interpreted as evidence for rapid evolution (e.g. Losos 2008). Here, we have demonstrated that even under a neutral model of biogeography, phylogenetic signal in climatic niches can take a wide range of values. Nonetheless, we show that signal is related to evolutionary processes. In our simulations migration strongly decreases phylogenetic signal under both speciation modes examined here. We also found that phylogenetic signal increased with the per-capita speciation rate, likely reflecting the shorter time available for migration between speciation events and perhaps also the higher power of λ on large trees (Münkemüller et al. 2012).

Therefore, we suggest that the phylogenetic signal in climatic niches observed in empirical studies could reflect more the history of species migration rather than the mode of evolution of physiological traits related to climatic tolerances. Empirical observations support this view both in mammals (Freckleton and Jetz 2009) and birds, where clades of sedentary birds have been shown to exhibit much higher phylogenetic signal in many climatic variables than clades composed of migratory species (Jetz et al. 2008).

Geographic speciation leads to punctuated niche evolution

Both speciation modes we examined result in daughter species inheriting different geographic distributions at speciation. Under point mutation, one of the two daughter species is restricted to only one location whereas its sister often has a larger range, while in the vicariance model both daughter species have by definition non-overlapping ranges immediately after speciation. This range disjunction between sister species directly translates into a difference in their mean climatic niches (Fig. 2). Whatever the spatial distribution of climate, model comparisons favored a punctuated mode of niche evolution over gradualist models, such as BM, which are typically assumed in most phylogenetic comparative methods (Fig. B.2). Even though our

simulations are simplistic, we believe that this conclusion tends to be generally true. Indeed, empirical and theoretical studies support the idea that speciation often involves some degree of geographic isolation (Coyne and Orr 2004), even in cases where speciation is ecological (Nosil 2012). Given that climate always exhibits a strong spatial structure, we suggest that speciation will almost always produce sister species with different mean climatic niches. However, this initial divergence implies no evolutionary change in physiology or ecology, it is simply a by-product of geographic separation. Punctuated evolution of climatic niches has indeed already been detected in alpine plants of the genus *Androsace* (Boucher et al. 2012), and niche shifts have been triggered by speciation following long-distance dispersal in the genus *Hordeum* (Jakob et al. 2010). Our results imply that evidence for punctuated evolution of climatic niches should not be directly interpreted as evidence for rapid evolution of physiological tolerances and even less as support for divergent selection on climatic attributes driving speciation. Indeed, physiological tolerances may remain unchanged even in the presence of apparent rapid change in the climatic niche.

Landscape boundaries create 'artefactual' niche conservatism

When comparing alternative models of niche evolution we found strong support for models that include a constraint (either OU or OUp) when migration was high. Under this scenario, regardless of the speciation mode, individuals move fast and therefore soon reach the borders of the landscape. This scenario approximates bounded Brownian motion and leads the mean climatic niches of species to be pulled back to the mean climate of the continent, thus producing outcomes similar to expectations of an OU process (Revell et al. 2008). Although our simulations are not able to represent the actual size and age of empirical metacommunities, we expect that OU models will be favoured when the

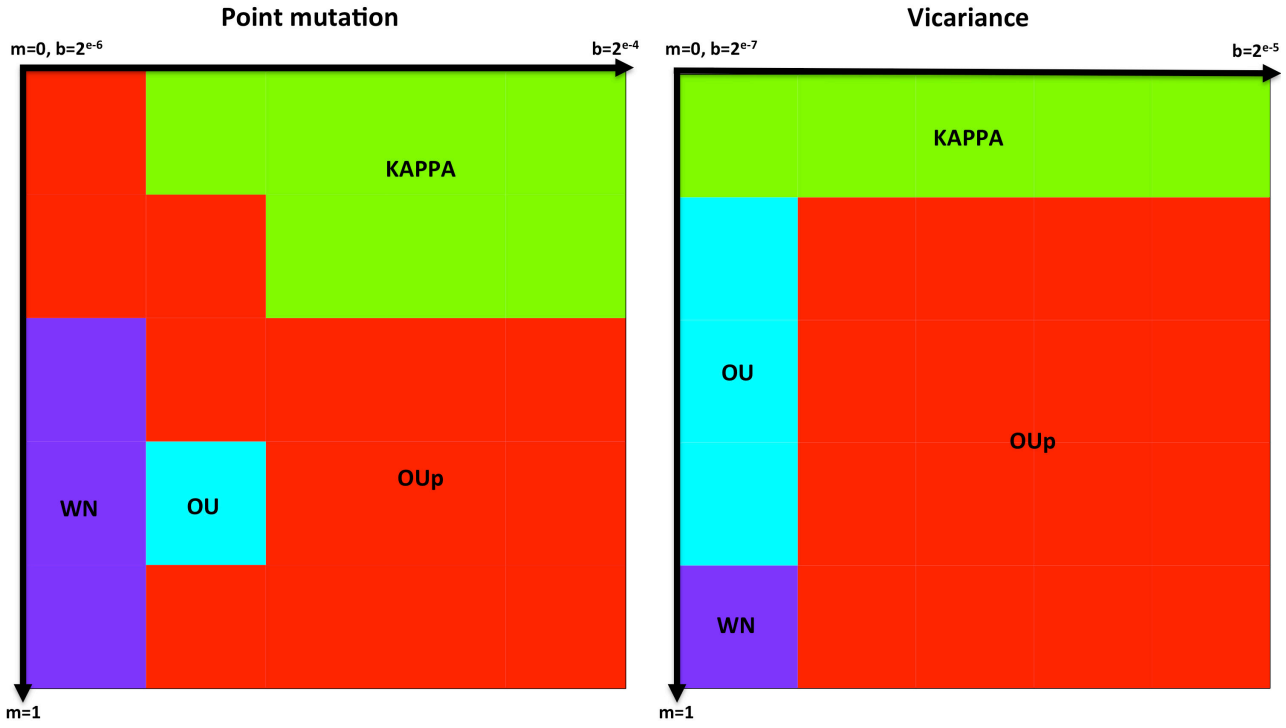

Figure 3. Comparison of NBT models to macroevolutionary models. For both speciation modes, the parameter values for migration and speciation rate are divided in 5 equal classes. In each of the 25 resulting cells, the model with the highest AICc weight on average over all simulations with the corresponding parameters is represented. See Appendix D for boxplots illustrating model comparison in each corner of the parameter space.

landscape is small, the clade is old and the migration rate is high. Furthermore, even when climate was not simulated according to a latitudinal gradient but rather taken from real, spatially auto-correlated landscapes, OU and OUp had still the best fit, even for relatively low migration rates. The OU process was initially applied to macroevolution to model adaptive evolution towards a given selective optima (Butler and King 2004), and is often interpreted as evidence for PNC (Wiens et al. 2010). However, our simulations favor an OU model even in the absence of selection. We follow Crisp & Cook (2012) in considering that such processes represent indirect causes that lead to 'artefactual' PNC, i.e. conservatism that is not a consequence of demo-genetic processes (Holt 1996).

To illustrate this point, we ran comparative analyses on *Diprotodontia,* a mammalian order that is restricted to Australia and Tasmania. We found that the best model depicting the phylogenetic patterns of their climatic niches was OUp. This case study demonstrates that BM can be easily rejected. Previously, we might have considered rejection of the BM model sufficient to conclude support for physiological constraints in *Diprotodontia* (i.e. niche conservatism), our simulations illustrate that this would be erroneous since the insular history of this clade alone could have created this pattern. Caution should then be taken when interpreting support for OU models for climatic niches in the absence of clear biological evidence for physiological constraints on species niches or stabilizing selection on some key ecological attributes. Indeed, it has already been shown that parameter estimates in OU models are often incompatible with the underlying quantitative genetic model (Harmon et al. 2010) and in addition, our study shows that similar patterns can arise through the migration of individuals in a bounded landscape with competition for space.

Which model to choose for climatic niche evolution?

Our results indicate that BM does not appropriately describe patterns of climatic niche evolution under a neutral model of biogeography because it fails to capture the punctuated and bounded nature of niche evolution. This limitation may be important because BM is often used in comparative studies either *a priori* as the default evolutionary model (e.g. Barnagaud et al. 2012; Pyron and Burbrink 2012) or because its few parameters make it likely to be favored over more complex models when the data contain insufficient information (Boettiger et al. 2012). In particular, assuming BM as the underlying model of niche evolution may lead to inflated Type I and Type II errors in tests of correlations between climate-related traits (Table 2). Our results suggest that a punctuated and/or bounded evolutionary model (i.e. OUp) might, in general, be more appropriate than BM for describing neutral climatic niche evolution, and that such models should be routinely included in comparative studies of niche evolution.

Limitations of our approach and future directions

Our study represents a first step towards a more mechanistic approach for the study of PNC and we are aware of several of its limitations. First, our results strongly supporting a model of punctuated niche evolution reflect our modeling of speciation as an instantaneous process. Although this assumption may be more or less accurate when viewed over geological timescales (Coyne and Orr 2004), simulations considering more subtle and process-informed speciation models (e.g. Desjardins-Proulx and Gravel 2012) would be needed to test the generality of punctuationism in niche evolution. Second, a more nuanced approach to simulating climate niches needs to be explored. Our simulations were deliberately simplistic so emphasize mechanisms, whereas reality is undoubtedly much more complex. Our goal here was especially to simulate climatic niche evolution resulting from purely neutral dynamics where realized species' niches are a product of dispersal and competition for space. We assumed that the physiological tolerances of species (i.e. their fundamental niches) were broad enough for individuals to occupy the whole landscape. Simulations in which the fundamental niche also evolves and influences individual fitness, while dispersal and ecological drift determine the realized niche of species,

might provide a step towards more realism. However, this would require assumptions on the way fundamental niches evolve, a topic on which very little research has been conducted (but see Kellermann et al. 2012).

We have shown how different processes (e.g. dispersal limitations and stabilizing selection) can lead to similar macroevolutionary patterns (e.g. PNC), thereby confirming previous claims that inferring processes from phylogenetic patterns can be challenging (Losos 2011). The search for potential factors or traits triggering or impeding climatic niche evolution may require additional information on species' ecology and physiology (e.g. inclusion information on life form to study the evolution towards cold niches in *Androsace* plants, Boucher et al. 2012). Fortunately, methods exist to fit flexible models with varying rates of evolution, strengths of selection and niche optima for different lineages depending on their biological characteristics (Beaulieu et al. 2012).

Conclusion

We do not suggest that the evolution of the climatic niche is solely driven by geographic processes, rather we simply demonstrate that common approaches to studying climatic niche evolution are affected by the geographic context in which a clade has evolved. Although our simulations may be relatively simplistic, we show that neutral models of biogeography produce very different outcomes than a commonly assumed neutral model of macroevolution (i.e. Brownian motion). We therefore suggest that punctuated and bounded models (e.g. OUp) rather than Brownian motion should be preferentially assumed as neutral models of climatic niche evolution. Such neutral models might constitute a reasonable first order approximation for the evolution of realized climatic niches upon which more elaborate models could be based. Critically, detecting the imprint of non-neutral ecological and evolutionary processes on the evolution of climatic niches will require additional biotic information, for example phenotypic traits directly linked to physiological tolerances.

ACKNOWLEDGMENTS

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CHAPITRE 2.

EVOLUTION DES NICHES CLIMATIQUES DANS LA NATURE : TEMPO, MODE ET CAUSES POTENTIELLES

Introduction

La façon dont les niches climatiques évoluent a d'importantes conséquences, en particulier pour la biogéographie historique (Wiens & Donoghue 2004, Jablonski et al. 2006). Malgré le nombre important de cas d'études qui ont été publiés sur la question, la diversité des méthodes utilisées empêche d'avoir des réponses claires sur les principales caractéristiques de l'évolution des niches climatiques. Dans l'article 2, nous avons assemblé un large jeu de données comprenant 125 clades de plantes, de mammifères, d'oiseaux et de poissons dans le but de fournir une vision d'ensemble de l'évolution des niches climatiques chez les plantes et les vertébrés.

Le résultat majeur que nous avons obtenu est que les niches climatiques n'évoluent généralement pas de manière graduelle au cours du temps, mais surtout par 'à-coups' entrecoupés de longues phases de stabilité. Les niches climatiques se conforment donc assez bien au modèle de l'équilibre ponctué.

En affinant notre analyse, nous avons confirmé que les niches climatiques évoluent principalement de manière ponctuelle puisque dans la grande majorité des groupes étudiés (117/125) le modèle le plus probable est un modèle d'Ornstein-Uhlenbeck à plusieurs optimaux. Ainsi, les niches restent contraintes et oscillent autour d'une valeur d'équilibre pendant des périodes de temps assez longues puis changent assez brusquement, en moyenne à un événement de spéciation sur huit. Ces brusques changements de niche ne sont donc pas aussi rares que certains l'avaient affirmé (Wiens et al. 2010) et prouvent que le PNC est répandu mais pas non plus omniprésent dans la nature.

La fréquence de changements de niche est très similaire entre plantes, oiseaux et mammifères, mais semble être causée par des facteurs différents dans chacun des groupes. Ainsi, chez les oiseaux, les clades dont les niches changent le moins souvent sont les clades tropicaux, alors que chez les mammifères ce sont les clades les plus jeunes, quelque soit leur distribution. Chez les plantes par contre, nous n'avons trouvé aucune variable expliquant la fréquence des changements de niche climatiques.

Cette étude est à ce jour la plus large à s'être intéressée à l'évolution des niches climatiques au cours des temps géologiques. Si elle a révélé un patron très général d'évolution

ponctuelle, elle souligne également que les causes sous-jacentes de l'évolution des niches climatiques sont multiples et varient fortement d'un groupe à l'autre.

ARTICLE 2

FAIBLE CONSERVATISME ET EVOLUTION PONCTUEE DE LA NICHE CLIMATIQUE CHEZ 125 GROUPES DE PLANTES ET DE VERTEBRES

PUNCTUATED EVOLUTION AND MODERATE PHYLOGENETIC NICHE CONSERVATISM ACROSS 125 CLADES OF PLANTS AND VERTEBRATES

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*: co-senior authors

The evolution of species' climatic niches is a fundamental process shaping past, present and future biodiversity patterns. Understanding phylogenetic niche conservatism (PNC), the tendency for species to retain ancestral niche characteristics over geological timescales[1], is thus crucial for anticipating species' range dynamics in face of environmental change[2]. Here we show across 125 clades of plants and vertebrates, that the climatic niche evolves mostly through rapid shifts associated with speciation events (punctuated equilibrium[3]). Climatic niche shifts occur on average in 1 out of 8 speciation events, demonstrating weaker levels of PNC than previously suggested[4]. Although the frequency of niche shifts was remarkably consistent across clades, drivers varied between groups. In birds, clades showing the strongest PNC are found in regions where climate has been the most stable over longer times [5], whereas in mammals, young clades show the strongest PNC. Our results demonstrate that climatic niche shifts have been frequent, but that they are associated with evolutionary divergences that might occur over much longer timescales than current rates of climate change.

In an era of environmental change, there has been a growing interest in the evolution of species' climatic niches[2], with considerable debate around the prevalence and causes of phylogenetic niche conservatism (PNC)[4,6], i.e. the tendency for species to retain ancestral niche characteristics[1]. Several hypotheses have been proposed to explain PNC, including environmental stability[5], dispersal limitations[7], competitive interactions[8], and lack of genetic variability[9] (see Supplementary Table S2). Because most studies to date have focused on relatively small geographic[10,11] or phylogenetic extents[12,13], there has not yet been a broad assessment of the prevalence of PNC[14] and its main causes[7]. Furthermore, it remains unknown whether climatic niches evolve gradually over time[15] or in rapid bursts following speciation events (punctuated equilibrium[3]). Recent methodological developments in comparative analysis combined with the increasing availability of species-level phylogenies and geographic distribution data allow us to explore for the first time general features of climatic niche evolution across multiple taxa and at a global scale.

We report here a comprehensive analysis of climatic niche evolution over 125 clades, comprising 6,470 species including birds, mammals, fishes and plants (Supplementary Table S1), which are widely distributed on Earth (Fig. 1). Two key climatic niche axes were jointly explored: mean annual temperature and annual precipitation for terrestrial organisms and minimum and mean sea-surface temperature for fishes. We first determined in each clade the degree of gradual vs. punctuated evolution in niche evolution. Second, we compared alternative models to find the most likely mode of niche evolution. We then used the most likely scenarios of niche evolution to assess the extent of PNC across our dataset and tested a range of potential drivers of PNC proposed earlier in the literature (see Table S2).

A very consistent pattern that emerged across clades is that climatic niches evolve largely through punctuated equilibrium (Fig. 2). Indeed, the median outcome across clades was that 88% of niche variance between species could be attributed to niche shifts associated with speciation rather than gradual change. In only few exceptions like the mammal genus *Tamias* (chipmunks, Fig. 1) and the bird genus *Muscicapa* (flycatchers), was niche evolution exclusively attributed to gradual evolution.

Comparing alternative models of climatic niche evolution, we found that simple models were usually rejected. Indeed, the Brownian motion model, where niches drift randomly over time, best fit the data in only 3 out of 125 clades, while a constrained model with a single optimum (Ornstein-Uhlenbeck model[16]) was detected in only 5 clades. More complex models where niches can shift between different selective regimes at speciation (*i.e.* Ornstein-Uhlenbeck models with multiple optima[17]) best fit the data for the remaining 117 clades (Fig. 2).

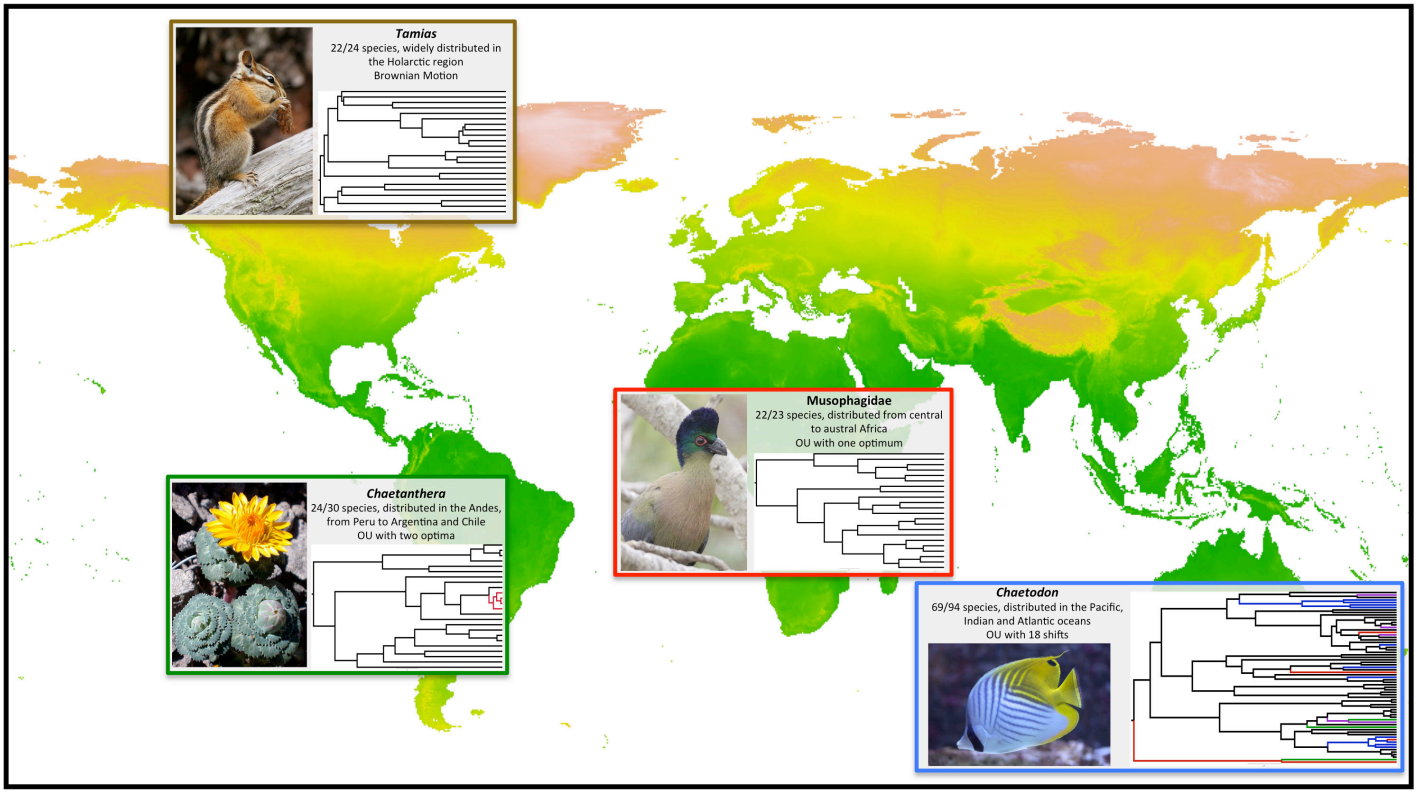

Figure 1. Contrasted examples of climatic niche evolution. The background shows a map of terrestrial mean annual temperature over the globe, brown colors show cold regions while green regions are the warmest. Results of model selection are shown for four clades, representative of the four major groups included in our study (plants, mammals, birds and fishes) and widely distributed on Earth. Coloured branches on phylogenies indicate different climatic optima. Photographs show members of the four clades: *Tamias minimus* (Wikipedia commons), *Chaetanthera flabellifolia* (S. Aubert/SAJF), *Tauraco porphyreocolus* (Wikipedia commons) and *Chaetodon auriga* (Wikipedia commons).

Because niche evolution generally did not proceed gradually, measuring evolutionary rates to assess the extent of PNC[18] was not appropriate. Instead, we used the proportion of nodes per clade where climatic niche shifts occurred as a measure of the strength of PNC. On average, shifts occurred at 13.2% of nodes (Fig. 2), indicating that PNC is common but not ubiquitous in nature. However, the frequency of niche shifts varied widely between clades; while some clades remained within a single selective regime during their whole history, niche shifts occurred at more than 25% of nodes in others (Fig. 1, Fig. 2). The proportion of shifts was similar amongst taxonomic classes, except for fishes, for which shifts occurred in more than 19% of nodes across the phylogeny. This high niche lability may in part be explained by the numerous transitions between coral reefs of different oceans that have occurred in Chaetodontidae and Labridae[19] (Fig. 1).

Strikingly similar levels of PNC shown by plants, birds and mammals (Fig. 2) were, however, associated with different factors. Overall, clades with larger geographic ranges showed stronger PNC (see Supplementary Figure S2). This result is mainly driven by clades occupying the Nearctic and Palearctic realms, where very large areas with relatively uniform climates may have allowed allopatric speciation with little niche divergence[20]. In birds however, clades occupying warmer regions tended to experience fewer niche shifts, suggesting that long-term climatic stability in the tropics is an important driver of PNC (Fig. 3, Supplementary Figure S2). Birds of the Musophagidae family (turacos) provide a good example: despite their wide distribution across sub-Saharan Africa, these 23 species evolved under the same climatic regime since their origin 56 Myr ago (Fig. 1). In contrast, historical variables were the most important in explaining PNC in mammals (Fig. 3, Supplementary Figure S2). Old clades tended to experience more shifts, possibly because they have undergone more climatic fluctuations in their history. Intriguingly, clades of mammals that diversified the fastest exhibited the strongest levels of PNC, perhaps because they represent adaptive radiations within a single climatic regime.

We also found that the number of potential competitors was positively associated with the level of PNC in both birds and mammals, which lends support to the notion that competition avoidance could be responsible for niche lability [21]. None of the variables linked to PNC in birds and mammals proved to be a good predictor of PNC for plants. Finally, contrary to some predictions[22], individual size was not related to PNC in any of the three groups.

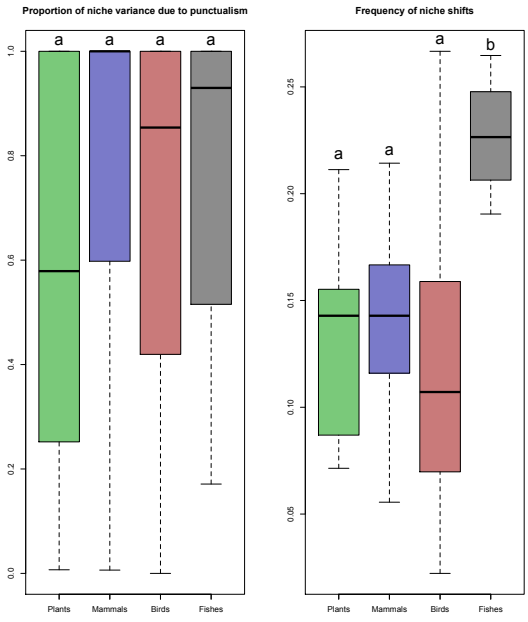

Figure 2. Left: proportion of variance between niches that can be associated with shifts at speciation, measured over both climatic axes combined. Right: frequency of climatic niche shifts, measured as the number of niche shifts over the number of nodes in the phylogeny each clade. For both measures, results over the 125 clades are presented separately for plants, mammals, birds and fishes.

Although our study does not embrace all major lineages of living organisms on Earth and is inherently limited regarding the mechanistic hypotheses currently available to test at such a large scale, it represents the most comprehensive global assessment of climatic niche evolution to date. We find that punctuated equilibrium is the dominant mode of climatic niche evolution, matching to theoretical predictions[23]. Our results show that while climatic niches remain relatively stable over long periods of time, a remarkably consistent proportion of speciation events (i.e. 1/8) lead to niche shifts. This pattern may arise because geographic separation at speciation indirectly induces shifts in the realized niche of newly formed species (Supplementary discussion). These results complement previous studies that demonstrated the ubiquity of biome conservatism[24] and suggests that PNC might be common but less pervasive at smaller climatic scales. Finally, although some large-scale biogeographic or historical variables explain part of the variation in the level of PNC between clades, we found that the main drivers of niche shifts are various and differ between major groups of organisms[7], and thus demonstrate that qualitatively similar diversity patterns[25] may have diverse underlying causes. Because speciation frequently occurs over timescales in the order of 10's to 100's of thousands of years, our results also have implications for adaptation to projected climate change, which is occurring at a rate that is over an order of magnitude faster.

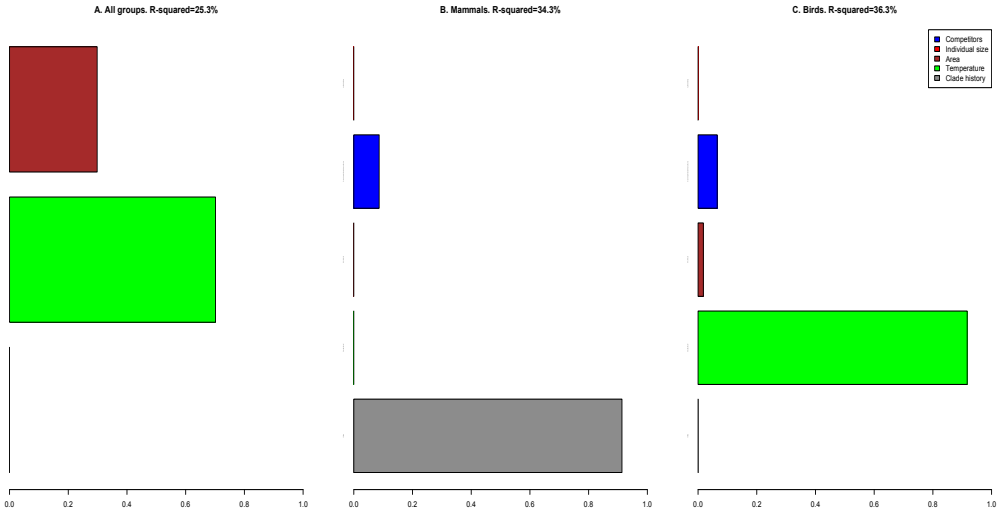

Figure 3. Relative importance of different hypotheses to explain PNC. These graphs show the relative importance of different groups of variables in random forests. Results for plants are not shown since no variable proved to be important. Fishes were excluded from this analysis since they were only 4 clades and do not share the same climatic variables as terrestrial groups. Temperature ariables are represented in green, area in brown, and competition in blue.

METHODS SUMMARY

Datasets were assembled from various sources with the criteria that both distribution data and phylogenetic dated trees resolved at species level should be available for at least 60% of described species in a clade. Clades containing less than 12 species were discarded. Species' climatic niches were measured by the mean species position along two climatic gradients over all locations where the species was recorded present. For terrestrial organisms, we extracted mean annual temperature and total annual precipitation from the Worldclim database[26] at a resolution of 10', whereas for fishes, minimum and mean annual sea-surface temperature were taken from the Bio-ORACLE database[27] at a resolution of 5'.

The degree of punctuated evolution of climatic niche positions on the two gradients was quantified using Ingram's ψ[28], .

Alternative macroevolutionary models for the evolution of climatic niches included Brownian motion[29] and Ornstein-Uhlenbeck models with multiple optima that were determined without any *a priori* on their position[30].

Because Ornstein-Uhlenbeck models with multiple optima almost always best fit the data, the degree of PNC in each clade was measured as the proportion of nodes in the phylogeny where shifts between different selective optima occurred. Correlates of the degree of PNC were explored using Random forests[31] with conditional computation[32] to account for correlations between predictors, and various mean clade traits (Supplementary Table S2, Supplementary Methods section 1.7.3.).

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SUPPLEMENTARY FIGURES AND TABLES

Taxonomic class	Studied clade	Number of species	Phylogenetic source	Species distribution source
Angiosperms	*Androsace* sect. *Aretia*, *Elongata* and *Septentrionalis*	34/34	Boucher et al. 2012[1]	Points: GBIF
Angiosperms	*Arctostaphylos*	39/65	Goldberg et al. 2011[2]	Points: GBIF
Angiosperms	*Babiana*	90/95	Schnitzler et al. 2012[3]	Points: herbaria
Angiosperms	*Capsicum*	15/25	Goldberg et al. 2010[4]	Points: GBIF
Angiosperms	*Ceanothus*	50/51	Goldberg et al. 2011[2]	Points: GBIF
Angiosperms	*Chaetanthera*	24/30	Hershkovitz et al. 2006[5]	Points: herbaria + P. Guerrero
Angiosperms	*Disa*	112/170	Bytebier et al. 2007[6]	Points: PRECIS
Angiosperms	*Euphorbia* sect. *Deuterocalli*, *Denisophorbia* and *Goniostema*	67/91	Aubriot 2012	Points: herbaria
Angiosperms	*Indigofera* Cape clade	35/41	Schrire et al. 2009[7]	Points: PRECIS
Angiosperms	*Lachnaea*	37/39	Beyers et al. 2001	Points: PRECIS
Angiosperms	*Leucadendron*	80/96	Tonnabel et al. in prep	Points: Protea Atlas
Angiosperms	*Leucocoryne*	17/17	Jara et al. 2013	Points: herbaria + P. Guerrero
Angiosperms	*Malesherbia*	24/25	Gengler-Nowak 2003[8]	Points: herbaria + P. Guerrero
Angiosperms	*Muraltia*	73/115	Forest et al. 2007[9]	Points: PRECIS
Angiosperms	*Nicotiana*	49/56	Goldberg et al. 2010[4]	Points: GBIF
Angiosperms	*Nolana*	72/89	Dillon et al. 2007[10]	Points: herbaria + P. Guerrero
Angiosperms	*Oenothera* sect. Anogra and Kleinia	18/19	Evans et al. 2009[11]	Points: herbaria
Angiosperms	*Pediomelum*	25/29	Egan et al. 2008[12]	Points: GBIF
Angiosperms	*Protea*	84/100	Valente et al. 2010[13]	Points: PRECIS
Angiosperms	Sarcolaenaceae	47/66	Haevermans et al. in prep	Points: herbaria
Gymnosperms	*Araucaria* sect. *Eutacta*	15/15	Leslie et al. 2012[14]	Points: GBIF
Gymnosperms	*Hesperocyparis*	14/17	Leslie et al. 2012[14]	Points: GBIF
Gymnosperms	*Juniperus*	46/50	Leslie et al. 2012[14]	Points: GBIF
Gymnosperms	*Picea*	29/33	Leslie et al. 2012[14]	Points: GBIF
Gymnosperms	*Pinus* subg. Pinus	56/71	Leslie et al. 2012[14]	
Gymnosperms	*Pinus* subg. Strobus	27/40	Leslie et al. 2012[14]	
Gymnosperms	*Podocarpus* subg. Podocarpus	29/42	Leslie et al. 2012[14]	Points: GBIF
Fishes	*Chadetodon*	69/94	Cowman et al. 2011[15]	Points: herbaria + litterature
Fishes	Chaetodontidae, bannerfish-corafish lineage	22/25	Cowman et al. 2011[15]	Points: herbaria + litterature
Fishes	Labridae tribe Labrines	19/23	Cowman et al. 2011[15]	Points: herbaria + litterature
Fishes	*Thalassoma* + *Gomphosus*	27/30	Cowman et al. 2011[15]	Points: herbaria + litterature
Mammals	Bovidae tribes Alcelaphalini and Hippotragini (African antelopes)	12/16	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Sciuridae subf. Xerinae tribe Protoxerini (African ground squirrels)	29/30	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Afrosoricida	42/42	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Pteropodide subf. Epomophorinae tribe Epomophorini	18/19	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Canidae	29/35	10kTrees[§]	Range maps: IUCN
Mammals	Musteloidea (=Ailuridae+Mephitidae+Mustelidae+ Procyonidae)	73/76	10kTrees[§]	Range maps: IUCN
Mammals	Cercopithecidae tribe Cercopithecini	22/30	10kTrees[§]	Range maps: IUCN
Mammals	Cervidae subf. Capreolinae tribe Rangiferini	16/16	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Cervidae subf. Cervinae tribe Cervini	12/15	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Colobinae	34/39	10kTrees[§]	Range maps: IUCN
Mammals	*Ctenomys*	37/38	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Dasyuromorphia	59/64	Pigot et al. 2012	Range maps: IUCN
Mammals	Didelphimorphia	53/84	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Diprotodontia	110/126	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Bovidae subf. Cephalophinae (duikers)	25/26	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Feliformia	83/97	10kTrees[§]	Range maps: IUCN
Mammals	Galagidae	14/18	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Geomydae	30/40	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	*Glauconycteris* + *Laephotis*	15/15	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Heteromyidae	57/64	Pigot et al. 2012[17]	Range maps: IUCN
Mammals	Hominoidae (*Homo sapiens* excluded[*])	16/24	10kTrees[§]	Range maps: IUCN
Mammals	Macroscelidea	15/17	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	*Murina* + *Harpiocephalus*	15/18	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Primates parvorder Platyrrhini (New world	59/67	10kTrees[§]	Range maps: IUCN

	monkeys)			
Mammals	*Ochotona*	23/30	Pigot et al. 2012[17]	Range maps: IUCN
Mammals	*Oligoryzomys*	14/18	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Peramelemorphia	15/18	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Perissodactyla	14/17	10kTrees[§]	Range maps: IUCN
Mammals	*Peromyscus*	36/56	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Phyllostomidae	144/150	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	*Pteropus*	41/65	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	*Reithrodontomys*	19/20	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Scandentia	17/19	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	*Sorex*	48/79	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	*Sylvilagus*	13/17	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	*Tamias*	22/24	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Cricetidae subf. Neotominae tribe Neotomini (woodrats)	16/23	Fritz et al. 2009[16]	Range maps: IUCN
Mammals	Xenarthra	29/29	Fritz et al. 2009[16]	Range maps: IUCN
Birds	Aegithalidae + Cettiidae + Phylloscopidae	91/116	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Accipitridae subf. Aegypiinae and Circaetinae	24/25	Hugall et al. 2012[19]	Range maps: Birdlife
Birds	Anatinae	108/123	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Anserinae	25/25	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Aquilinae	29/35	Hugall et al. 2012[19]	Range maps: Birdlife
Birds	*Basileuterus* + *Cardellina* + *Ergaticus* + *Wilsonia pusilla* + *Myioborus* + *Phaeothlypis*	40/43	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Campephagidae	70/80	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Caprimulgidae	51/70	Hugall et al. 2012[19]	Range maps: Birdlife
Birds	*Carduelis* group Spinus	17/19	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Cercomacra* + *Myrmeciza* + *Drymophila* + *Hypocnemis*	22/30	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Cercomela* + *Oenanthe* + *Myrmecocichla*	35/37	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Ciconiidae	16/19	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Cossypha* + *Cossyphicula* + *Alethe* + *Sheppardia*	26/29	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Cracidae	36/50	Pigot et al. 2012	Range maps: Birdlife
Birds	*Conothraupis* + *Volatinia* + *Lanio* + *Ramphocelus* + *Coryphospingus* + *Tachyphonus* + *Rhodospingus* + *Eucometis* + *Trichothraupis* (crested tanagers)	28/30	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Cuculidae	125/142	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Dendroica* + *Wilsonia citrina* + *Catharopeza* + *Parula* + *Setophaga*	32/35	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Diglossa*	18/18	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Elaenia* and allies (see dataset[+])	76/89	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Emberiza*	36/44	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Empidonax*	15/15	Pigot et al. 2012[17]	Range maps: Birdlife
Birds	Eurylaimidae + Pittidae	44/52	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Falconidae	49/65	Hugall et al. 2012[19]	Range maps: Birdlife
Birds	*Ficedula*	25/31	Pigot et al. 2012[17]	Range maps: Birdlife
Birds	Furnariidae subf. Dendrocolaptinae	45/60	Derryberry et al. 2011[20]	Range maps: Birdlife
Birds	Furnariidae subf. Scelurinae	17/17	Derryberry et al. 2011[20]	Range maps: Birdlife
Birds	Furnariidae subf. Furnariinae tribe Synallaxini	113/122	Derryberry et al. 2011[20]	Range maps: Birdlife
Birds	Furnariidae subf. Furnariinae tribes Philydorini and Furnariini	74/76	Derryberry et al. 2011[20]	Range maps: Birdlife
Birds	Gruidae	11/15	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Hirundinidae	76/83	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Icteridae	91/102	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Muscisaxicola* + *Lessonia* + *Knipolegus* + *Hymenops* + *Satrapa*	25/26	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Charadriiformes suborder Lari	122/149	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Maluridae	21/27	Pigot et al. 2012[17]	Range maps: Birdlife
Birds	*Merops*	22/24	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Muscicapa*	25/25	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Musophagidae	22/23	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Myrmotherula*	22/30	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Oriolus* + *Sphecotheres* + *Paramythia* + *Pitohui*	30/34	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Otididae	24/25	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Pachycephalidae subf. Pachycephalinae	33/44	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Paridae + Stenostiridae	54/70	Jetz et al. 2012[18]	Range maps: Birdlife

Birds	Accipitridae subf. Perninae and Gypaetinae	15/19	Hugall et al. 2012[19]	Range maps: Birdlife
Birds	Petroicidae	33/44	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Phasianidae	99/140	Hugall et al. 2012[19]	Range maps: Birdlife
Birds	Picnonotidae	94/128	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Pipridae	41/51	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Poospiza* + *Hemispingus* + *Pyrrhocoma* + *Thlypopsis* + *Cnemoscopus* + *Nephelornis* + *Donacospiza* + *Compsospiza* + *Cypsnagra*	30/39	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Charadriiformes suborder Scolopaci	82/105	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Sturnus* and allies (see dataset[+])	130/130	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Tangara* and allies (see dataset[+])	138/155	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Thamnophilus* + *Sakesphorus*	31/33	Pigot et al. 2012[17]	Range maps: Birdlife
Birds	Tityridae	26/29	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	Trogonidae	39/43	Jetz et al. 2012[18]	Range maps: Birdlife
Birds	*Turdus*	64/78	Pigot et al. 2012[17]	Range maps: Birdlife
Birds	*Tyrannus* + *Machetornis* + *Pitangus* + *Myiozetetes* + *Empidonomus* + *Myiodynastes* + *Megarynchus*	21/28	Jetz et al. 2012[18]	Range maps: Birdlife

Supplementary Table S1: Presentation of the 125 clades included in our dataset. The taxonomic class of each group is presented in the first column, plants have been divided into gymnosperms and angiosperms. The description of each clade is given as a list of the different taxonomic categories that it encompasses. The third column indicates the number of species that were included in our analyses and the number of species estimated by taxonomists for each clade. Sources for the phylogeny and species distribution data are presented in the two last columns.

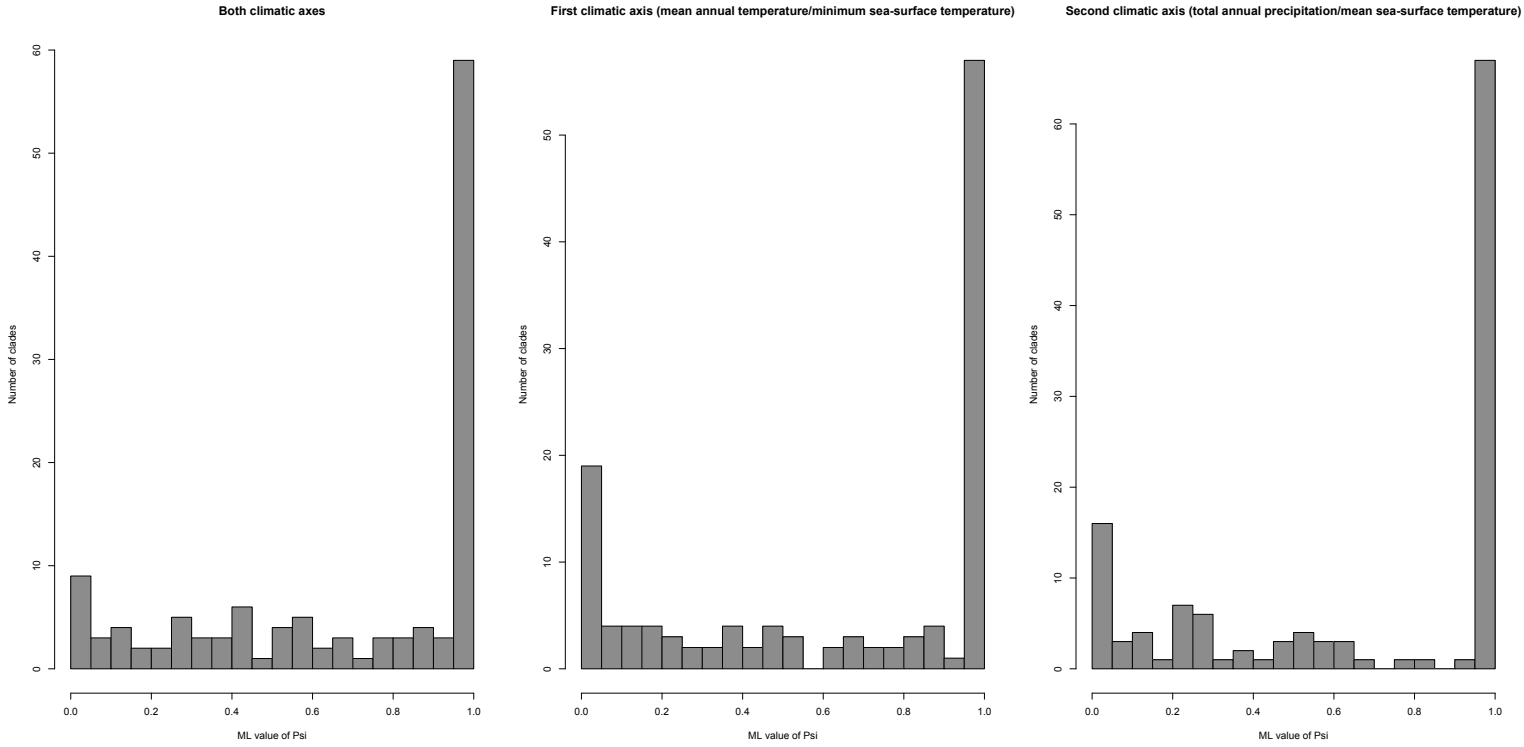
[§]: 10ktrees website: 10ktrees.fas.harvard.edu; Arnold, Matthews and Nunn 2010. Consensus trees for each group were downloaded in November 2012.

[*]: *Homo sapiens* was excluded from the analysis since his niche may not be affected by climatic variables anymore.

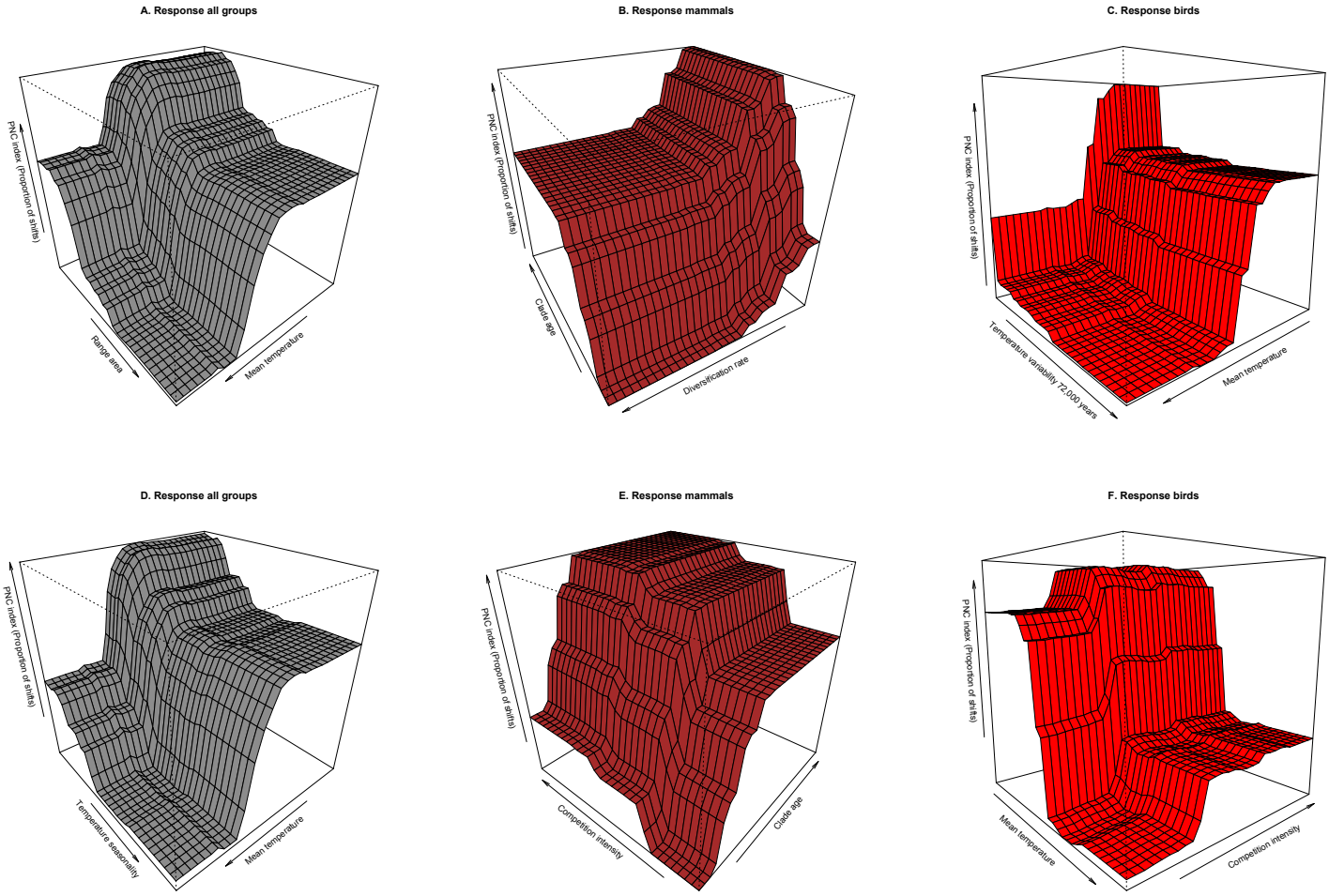
[+]: These three groups contain species from a lot of different genera that could not all be enumerated in this table.

Hypothesis	Description	Proxy
Environmental stability	Both short-term (i.e. year-round) and long-term environmental stability should lead to stabilizing selection on the climatic niche, and thus PNC[21,22]. Such stability should be predominant in the tropics, as stated by the 'Tropical Niche Conservatism' hypothesis[23].	Short-term climatic stability was measured as the average temperature seasonality (bio4 variable, Hijmans et al. 2005) over each clade's range. Mid-term climatic stability was measured as the variance in mean annual temperature over the last 72,000 years. Finally, in the absence of of detailed data on deep past climates, we used current mean annual temperature as a proxy for long-term climatic stability.
Dispersal limitation	The climatic niche of a species could be conserved simply because new climates cannot be accessed because of dispersal limitations, even in cases where physiological characteristics would make adaptation to new climates possible[24].	The area (km^2) of the range of each clade was taken as a measure of dispersal opportunity.
Competitive interactions	Competition can have opposite effects on PNC: on the one hand stabilizing selection could occur if competitors prevent a species from adapting to new environments[25], while on the other hand competition avoidance could lead to divergent selection on the climatic niche to avoid sympatry[26,27].	We measured the intensity of competition for each clade of birds (or mammals) as the average richness of other birds (or mammals) over the clade's range using range maps provided by BirdLife and the IUCN. Clades of carnivorous species were given no value (i.e. NA) since other species more likely are preys than competitors. For plants, the average Net Primary Productivity over each clade's range was used as an index of competition intensity.
Individual size	Animals and plants with large body sizes tend to have slower rates of molecular evolution due to lower metabolic rates[28] and longer generation times[29]. This should lead them to have lower levels of genetic variability, a pattern that could cause PNC[30].	For clades of bird and animals, average body mass of species was used to characterize body size in each clade. Values were log-transformed. The PanTHERIA database[31] was used for mammals, while W. Jetz kindly provided data for birds. For plants, in the absence of information on height for most of the clades we retained, clades were classified as being either primarily woody or herbaceous[32], which traduces major differences in height.

Supplementary Table S2: Hypotheses to explain PNC. This table presents four main hypotheses that have been proposed to explain PNC and that we tested. Each hypothesis is described and the proxy that we used is presented. Unfortunately, hypotheses linked to population genetics could not be tested on such a large dataset because of data unavailability (see Supplementary Methods section 1.7.)



Supplementary Figure S1: distribution of ψ over the 125 clades included in our study. From left to right, ML estimates of ψ on both niche axes combined, the first axis and the second axis are presented. A value of 0 indicates purely gradual evolution, while a value of 1 indicates purely punctual evolution.



Supplementary Figure S2: influence of different variables on the level of PNC. These plots show the value of our PNC index predicted by the two best predictors (1st row) or the first and third best predictors (2nd row) in all groups combined, mammals and birds. A. Response to range area and mean temperature among all groups (n=113). B. Response of PNC to mean diversification rate and clade age for mammals (n=30). C. Response of PNC to temperature variability over the last 72,000 years and mean temperature for birds (n=51). D. Response to temperature seasonality and mean temperature among all groups (n=113). E. Response of PNC to competition intensity and clade age for mammals (n=30). F. Response of PNC to competition intensity and mean temperature for birds (n=51). Other variables were fixed to their mean value among the dataset for predicting the PNC index from random forest models. Results for plants are not presented since no variable was a good predictor of the PNC index. Fishes were excluded from this analysis since they were only 4 clades and do not share the same climatic variables as terrestrial groups.

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CHAPITRE 3.

L'HISTOIRE DU GENRE *ANDROSACE*, UN EXEMPLE POUR LA COMPREHENSION DES ORIGINES DE LA FLORE ALPINE

Introduction

Après deux premiers chapitres dédiés à des questions méthodologiques et au test de concepts généraux, les deux derniers chapitres de ma thèse sont consacrés à la flore alpine.

Dans ce chapitre, nous nous sommes intéressés à un groupe de plantes emblématique de la Flore des Alpes : le genre *Androsace* L. (Primulaceae). Il existe environ 110 espèces d'androsaces, réparties dans toutes les zones tempérées, alpines et arctiques de l'hémisphère nord. Les plantes de ce genre ont des formes de vies diverses, allant des annuelles ou bisannuelles à des plantes en coussin dont la longévité est élevée (plusieurs dizaines d'années). Mis à part ces différences de forme de vie, les androsaces sont assez homogènes dans leur écologie : elles sont toutes d'assez mauvaises compétitrices, sont homostyles et ont des fleurs blanches ou roses (sauf *Vitaliana primuliflora* dont les fleurs sont jaunes et hétérostyles). Beaucoup d'espèces sont endémiques de divers massifs de la chaîne Alpide (massifs montagneux du Sud de l'Eurasie, allant des Pyrénées à l'Himalaya).

Androsace est un exemple idéal pour étudier l'histoire de la flore alpine et en particulier l'adaptation aux milieux froids. Nous y avons étudié en détail l'apparition de la forme de vie en coussin ainsi que son influence sur l'évolution des niches climatiques. Cette étude est présentée dans l'article 3.1. et démontre que la forme de vie en coussin est une innovation clef (*sensu* Miller 1949) chez *Androsace*, qui est apparue au moins deux fois de manière indépendante en Himalaya et dans les Alpes et a ensuite permis de coloniser les environnements alpins. En nous basant sur ces résultats, nous avons proposé un scenario pour l'évolution de la tolérance au froid chez *Androsace*, qui peut être résumé comme suit. Les ancêtres du genre, probablement déjà adaptés aux conditions tempérées des steppes froides, ont été progressivement 'soulevés' par l'orogénèse de la chaîne Alpide. L'isolation croissante sur ces îlots montagneux combinée à de faibles capacités de dispersion a empêché certaines espèces de retourner vers les habitats de plaine qui leur étaient favorables et les a au contraire contraintes à s'adapter au climat local. Sous ces fortes pressions de sélection pour une tolérance accrue au froid, la forme de vie en coussin est apparue et a permis la colonisation des habitats alpins fraîchement apparus. La généralité de ce scénario pour l'évolution de la flore alpine reste bien sûr à tester de manière fine sur

d'autres groupes, mais le chapitre 4 de ma thèse en confirme les grandes lignes pour la majorité des espèces en coussin.

Ensuite, nous nous sommes intéressés à la biogéographie historique et à la diversification du genre *Androsace.* La richesse et la large distribution du genre *Androsace* sont en effet étonnantes puisque les trois processus biogéographiques majeurs (i.e. spéciation, extinction et migration, Ricklefs 2004) semblent jouer contre le succès évolutif de ce groupe:

- les environnements froids qu'occupent les androsaces entraînent des taux métaboliques faibles et en particulier les taux de spéciation devraient y être assez lents (Wright et al. 2006)

- la longévité des androsaces pourrait compromettre leurs capacités d'adaptation face aux changements de l'environnement et conduire à des taux d'extinction élevés

- les faibles capacités de dispersion des espèces d'androsaces en coussin (Anderberg & Kelso 1996) combinées à la fragmentation des habitats alpins et à la présence de nombreuses endémiques dans le genre devraient limiter les opportunités de migration entre différentes régions.

Dans l'article 3.2., nous avons abordé ces questions et proposé des explications pour le succès évolutif du genre *Androsace*. Nous avons en particulier montré que différentes formes de vies ont eu des rôles complémentaires dans l'histoire du genre : dans un premier temps, des espèces annuelles asiatiques adaptées aux steppes froides ont en effet permis de coloniser l'Europe de l'Ouest ; ensuite, la forme de vie en coussin apparue indépendamment en Himalaya et dans les Alpes a accéléré la diversification du genre, probablement en offrant plus d'opportunités de spéciation allopatrique dans les habitats alpins fragmentés.

Ces deux études que nous avons menées sur le genre *Androsace* permettent de mieux comprendre les grandes lignes de l'histoire de ce genre, de la colonisation des environnements alpins à sa diversification.

ARTICLE 3.1

ORIGINES DES NICHES ALPINES ET DE LA FORME DE VIE EN COUSSIN DANS LE GENRE *ANDROSACE*

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RECONSTRUCTING THE ORIGINS OF HIGH-ALPINE NICHES AND CUSHION LIFE FORM IN THE GENUS *ANDROSACE S.L.* (PRIMULACEAE)

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Relatively, few species have been able to colonize extremely cold alpine environments. We investigate the role played by the cushion life form in the evolution of climatic niches in the plant genus *Androsace s.l.*, which spreads across the mountain ranges of the Northern Hemisphere. Using robust methods that account for phylogenetic uncertainty, intraspecific variability of climatic requirements and different life-history evolution scenarios, we show that climatic niches of *Androsace s.l.* exhibit low phylogenetic signal and that they evolved relatively recently and punctually. Models of niche evolution fitted onto phylogenies show that the cushion life form has been a key innovation providing the opportunity to occupy extremely cold environments, thus contributing to rapid climatic niche diversification in the genus *Androsace s.l*. We then propose a plausible scenario for the adaptation of plants to alpine habitats.

KEY WORDS: Alpine plants, climatic niche, key innovation, niche conservatism, phylogenetic signal, phylogenetic uncertainty

The evolutionary mechanisms that drive species' ranges have fascinated evolutionists and biogeographers since Darwin (1859). One key element lying at the heart of these questions is the set of ecological conditions required for a given species to maintain viable populations (i.e., the species' ecological niche, Grinnell 1917; Hutchinson 1957). Among the different niche dimensions, climatic niches are particularly interesting in the current context of climate change, because their evolutionary stasis (i.e., niche conservatism) combined with insufficient migration capacities (Loarie et al. 2009), could lead to disproportionate species loss in certain clades (Mace et al. 2003; Parmesan 2006; Thuiller et al. 2011). Recent literature emphasizes that there is an urgent need to test whether niche conservatism can be considered as a general principle (Wiens et al. 2010), and to determine the rates and drivers of climatic niche evolution (Lavergne et al. 2010a).

Despite the current debate on the prevalence of niche conservatism in nature (Losos 2008a; Wiens et al. 2010), some general principles have been identified. The most common view is that

high dispersal rates in a species enable habitat selection, leading to stabilizing selection on key ecological traits and hence niche conservatism. Donoghue (2008) posited that it might be easier and quicker for species to migrate than to evolve when exposed to environmental change. In contrast, situations suited for rapid niche evolution often involve dispersal limitations. Ackerly (2003) pointed out that isolation on "environmental islands" subject to environmental change might expose species to strong selection pressures, resulting in punctual and abrupt niche shifts. The literature on adaptive radiations contains numerous examples of rapid niche evolution in insular settings (e.g., Witter and Carr 1988; Pinto et al. 2008). Most of these cases involve the emergence of a key innovation, that is, a trait that allows a species to interact with the environment in a fundamentally different way and provides the stimulus for niche evolution (Miller 1949; Losos and Mahler 2010; we do not use in this article the recent definition of a key innovation as a trait enhancing diversification rates).

A commonly used approach for testing niche conservatism has been the measurement of "phylogenetic signal." This statistical pattern measures "the tendency for related species to resemble each other more than if they were taken at random from a phylogenetic tree" (Blomberg and Garland 2002), a strong phylogenetic signal in niche-related traits being usually interpreted as evidence for niche conservatism (Losos 2008a). However, although phylogenetic signal describes a statistical pattern of trait autocorrelation across phylogenies, it is not useful for inferring the rate (amount of change per unit of time), the tempo (early vs. late) and the mode (punctual vs. gradual) of niche evolution (Revell et al. 2008; Lavergne et al. 2010a). Recently, Evans et al. (2009) investigated the tempo (i.e., early vs. late) of climatic niche diversification in a group of plants (*Oenothera* spp. [Onagraceae], sections *Anogra* and *Kleinia*) and showed that comparing niche evolutionary patterns to the ones expected under a null model of Brownian evolution can reveal interesting insights into the processes driving niche evolution (see also Yesson and Culham 2006a,b). Surprisingly, little attention has been paid to the biological traits potentially driving niche evolution (but see Luxbacher and Knouft 2009; Edwards and Smith 2010). Indeed, most of the studies on climatic niche conservatism have detected patterns of niche evolution and in some cases have discussed their consequences, but have rarely tackled the processes that are directly involved (Wiens et al. 2010).

Alpine species are well suited to the study of niche evolution because they have experienced major climatic fluctuations in the past (Zachos et al. 2008), and may exhibit key phenotypic innovations that have allowed the colonization of alpine niches following mountain uplifts. Moreover, the mountain ranges they occupy make their distribution highly fragmented and their survival particularly vulnerable to climate change (Randin et al. 2009). Here, we focus on the *Androsace* (sensu Martins et al. 2003) genus (Primulaceae), a group of about 110 species (according to the International Plant Names Index, http://www.ipni.org) and distributed among the temperate and cold regions of the Northern Hemisphere, many of them being endemic to certain mountain ranges. It is suspected that the evolutionary history of *Androsace* has been primarily shaped by mountains uplifts and past climate fluctuations, as already detected in some groups in which floras have been fragmented by the emergence of high-altitude island-like habitats (e.g., Hughes and Eastwood 2006). Interestingly, species within this genus harbor a variety of life forms, such as annual and perennial herbaceous, but also long-lived cushions, which have long been thought to be adapted to harsh alpine conditions (Körner 1999). However, the link between life form and particular climatic niches has never been quantitatively tested.

This leads us to address the following questions: (1) is there any trace of past rapid climatic niche evolution in *Androsace*, as expected given the fragmentation of the high-altitude habitats they occupy? (2) Is the cushion life-form ancestral in *Androsace* or is it a derived character? And if derived, when and how many times has it evolved? (3) Is the cushion life form a key innovation (sensu Miller 1949) that triggered a significant shift toward alpine niches? To answer these questions and understand the evolutionary history of climatic niches and life forms in the *Androsace* genus, we developed a comprehensive phylo-climatic modeling approach. We first built the most complete phylogeny of the *Androsace* genus to date. Then, we used robust methods to estimate species' climatic niches and compared them in the phylogenetic framework while accounting for intraspecific niche variability, and uncertainty in phylogenetic inference and ancestral traits reconstructions.

Material and Methods

STUDY GROUP AND TAXON SAMPLING

Recent phylogenetic studies (Martins et al. 2003; Schneeweiss et al. 2004) have shown that the former *Androsace* L., *Vitaliana* Sesl., *Douglasia* Lindl., and *Pomatosace* Maxim. genera form a monophyletic group (hereafter referred to as the *Androsace* genus). The hotspot of species richness for *Androsace* occurs in the Eastern Himalaya, as for Primulaceae in general, suggesting that this clade is of Asian origin. All *Androsace* species except *Vitaliana primuliflora* are characterized by white or pink homostylous flowers that have a short corolla tube and are relatively large compared to plant size (Ruffier-Lanche 1964). They are mainly pollinated by Hymenoptera and have low competition abilities. The main differences between species of the genus are their contrasted soil ecologies (e.g., *Androsace alpina* is described as mainly silicicolous and *A. helvetica* as mainly calcicolous, Lauber and Wagner 2007), their climatic

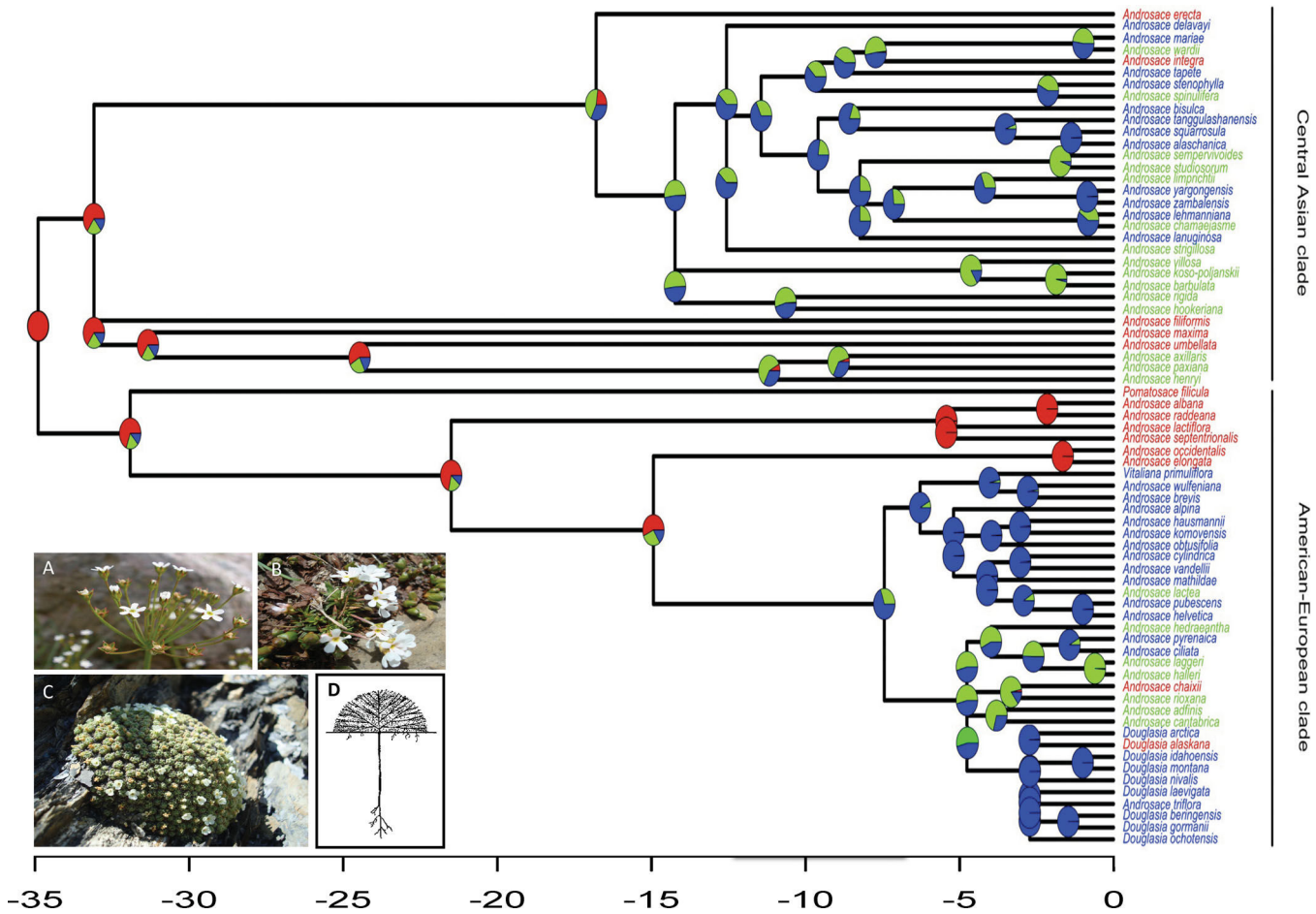

Figure 1. **Evolution of life forms in the *Androsace* genus. The tree is the consensus tree for 71 species of the genus, with the time scale given in million years. Two main clades segregate from the root. Each ancestral node is colored according to the marginal likelihoods of the different life forms in the NEJ-root model (red = short-lived; green = perennial; blue = cushion). Tips are colored the same way. The cushion life form appears independently in the two main clades. Photographs show representatives of the different life forms. (A) *A. septentrionalis*, short-lived (annual, photo: S. Aubert/SAJF). (B) *A. adfinis*, perennial (photo: F.Boucher/LECA). (C) *A. helvetica*, cushion (photo: F. Boucher/LECA). (D) Schematic representation of the cushion morphology, with its dense canopy formed by radial ramifications (illustration in R. Ruffier-Lanche 1964).**

requirements (from dry steppes to mountain tops) and their different life forms, ranging from annual species to cushions with high individual longevity (see illustrations on Fig. 1).

The phylogenetic trees we built contain 77 taxa (see Appendix S1). Subspecies were first collapsed together (always collapsed to the type subspecies) as the occurrence data we used did not distinguish between subspecies (71 species left). All the species were used to estimate ancestral life forms. Finally, 19 species were pruned from the trees and removed from the analyses on climatic niches, as there was little knowledge about their current distribution (fewer than five known occurrences, see list in Appendix S1).

PHYLOGENETIC INFERENCE

All ITS and trnL-F sequences available in Genbank for *Androsace*, *Douglasia*, *Potamosace*, and *Vitaliana* plus three outgroups (*Soldanella alpina* L., *Trientalis borealis* Raf., and *T. europaea* L.) were retrieved (accession numbers available in Appendix S1). Both regions were available for 61 ingroup species (66 taxa including subspecies), and only one region was available for 11 additional species, thus covering around 65% (72 out of ca. 110) of the *Androsace* species. Those sequences correspond to the following studies: Dixon et al. (2009), Martins et al. (2003), Mast et al. (2006), Schneeweiss et al. (2004), Schönswetter and Schneeweiss (2009), Wang et al. (2004). When more than one sequence was available for each taxa and region, a consensus sequence was created with Bioedit (Hall 1999). For each region, sequences were aligned with ClustalW2 (Larkin et al. 2007), Kalign (Lassmann and Sonnhammer 2005), MAFFT (Katoh et al. 2005), and Muscle (Edgar 2004). The best alignment was chosen with the multiple overlap score of MUMSA (Lassmann and Sonnhammer 2006). MUMSA is a tool for automatic assessment of alignment quality

that provides two indices: the average overlap score, which indicates whether the sequences cumulated for a region are too divergent to be aligned consistently; and the multiple overlap score, which identifies the most consistent alignment when comparing different alignments for a same set of sequences. For both regions, the best alignment was the one produced by MAFFT. We removed ambiguous sites from the alignments matrices with trimAl using the heuristic algorithm—*automated1* (Capella-Gutierrez et al. 2009), which uses gaps and similarities distribution to determine the thresholds for trimming the poorly aligned sites of an alignment. We determined the best-fitting model of evolution for each region with the Akaike Information Criterion (AIC) as implemented in MrModeltest version 2 (Nylander 2004). Both regions were concatenated with FASconCAT (Kuck and Meusemann 2010). Phylogenetic analyses were conducted for the combined dataset with MrBayes 3.1.2. (Ronquist and Huelsenbeck 2003) with partitioned model parameters for each region. Two independent analyses were run with 20 million generations sampling one of every 100 trees. Run convergences were checked with AWTY (Nylander et al. 2008), a tool for graphical exploration of convergence in rates of posterior split probabilities and branch lengths. The first 25% of trees were eliminated in the *burn-in* phase. The combined matrix and the 50% majority-rule consensus phylogenetic tree were deposited in Treebase; study number TB2:S11159 (http://www.treebase.org).

Dating analyses were performed with PAML (Yang 1997) and Multidivtime packages (Kishino et al. 2001; Thorne and Kishino 2002), which provide a mean age and a 95% confidence interval (95% CI) for each node. This was applied to 100 randomly selected trees from the posterior distribution of Bayesian analyses to take into account phylogenetic uncertainty in subsequent analyses. To calibrate the trees, due to the lack of a suitable fossil record for *Androsace*, a minimum and maximum age constraint (34.5–35.3 million years ago [Mya]) was applied to the *Androsace* crown node based on the results (95% CI limits) obtained in Yesson et al. (2009), which produced a dated generic level molecular phylogeny of Primulaceae and Myrsinaceae. A maximum age of 45.3 Mya was applied to the root node, which corresponds to the upper limit of the 95% CI (Yesson et al. 2009) for the split between Primulaceae and Myrsinaceae (to which *Trientalis* belongs). We used the ages reported by Yesson et al. (2009) and not those of Schneeweiss et al. (2004) because we consider the data of the former are more accurate. Schneeweiss et al. (2004) dating was indeed based on divergence estimates of Maesaceae, Theophrastaceae, Primulaceae, and Myrsinaceae obtained by Wikström et al. (2001) in a study including only two genera of Primulaceae, whereas Yesson et al. (2009) constructed expressly a phylogeny of Myrsinaceae (18 genera included) and Primulaceae to obtain a secondary age estimate for the genera of Primulaceae (13 genera sampled).

For the following analyses, each of the 100 trees was pruned to keep only 62 (for life-form reconstructions) or 51 tips (for all calculations including climatic niches) using PAUP* 4.0b10 (Swofford 2002).

LOCATION

Occurrence data for 51 species of *Androsace* (see list in Appendix S1) were extracted from the Global Biodiversity Information Facility database (GBIF, http://www.gbif.org). Occurrences for 13 species from the Alps obtained from two French National Botanical Conservatories (CBNA, http://www.cbna05.com, and CBNMED, http://www.cbnmed.fr) and from the CRSF Swiss Floristics Network (http://www.crsf.ch) were also added to the dataset. After deleting all points with coordinate precisions lower than 0.01 arc-degree, more than 7000 points remained almost equally distributed between the two different data sources. European species were generally more represented in the data than Central Asian and American ones (see number of occurrences for each species in Appendix S1). As no additional sources of distribution data are available for the Asian part of the study, and because our results were robust to the low number of occurrence for some species (Appendix S2), this data asymmetry is not likely to generate any bias in our study but should only reduce the statistical power of interspecific comparisons of niche characteristics

NICHE SEPARATION

To separate species' niches in a multidimensional space, we used an ordination method called the "outlying mean index" (OMI, Dolédec et al. 2000), which measures the distance between a species' niche and the mean conditions of the sampling area (in this case, all locations where *Androsace* species are present). Unlike other ordination techniques, the OMI makes no assumption about the shape of the species' response curve to environmental gradients and gives equal weight to all sites regardless of their species richness (Thuiller et al. 2004). The latter characteristic was particularly appreciable in our case, given the low number of observed occurrences in Central Asia.

Global climate across the Northern Hemisphere was represented by the 19 "Bioclim" variables from the WORLDCLIM database (Hijmans et al. 2005, http://worldclim.org) for the baseline period (1950–2000). These variables represented a range of metrics (mean value, variance, and extremes) on global temperature and precipitations. The topographic heterogeneity of the mountain ranges where *Androsace* mostly occurs and the average precision of the occurrence data led us to choose a moderate resolution of 2.5′. We also added a critical variable for plant physiology, namely the ratio of actual over potential evapotranspiration (aetpet, see Thuiller et al. 2005 for more details). The choice of including only climatic variables into the niche estimation was motivated by the global scale of our study, at which it is

known that primary determinants of species distributions are climatic (Woodward 1990, 1992). Furthermore, in the special case of *Androsace*, which share similar biotic interactions and occur in relatively cold and dry environments, abiotic variables might be more important than biotic ones for setting niche boundaries (Körner 1999). Although *Androsace* species show contrasting soil ecologies, and even if substrate type strongly influences alpine plant distributions (Alvarez et al. 2009), we did not include soil preferences in our study due to the absence of data with a sufficient global scale resolution.

INTEGRATING MULTIPLE SOURCES OF UNCERTAINTY

In this study, we developed an original workflow to account for multiple sources of uncertainty (Appendix S4).

(1) To date, few studies of niche evolution have explicitly incorporated phylogenetic uncertainty through the use of multiple phylogenetic trees (but see Edwards and Smith 2010). Here, all subsequent analyses were carried out on a set of 100 phylogenetic trees sampled randomly from the stationary phase of Bayesian analyses.

(2) Another possible source of error is due to the fact that most comparative studies often consider only the mean value of a character for each species (Losos 2008a; Kozak and Wiens 2010). Indeed, evolutionary biologists since Darwin (1859) have known about intraspecific variability in niche-related traits, as it is the basis of lineage differentiation and speciation. It can sometimes be higher than interspecific variation among closely related species (Felsenstein 2008; Albert et al. 2010) and can inflate type I errors in phylogenetic tests (Harmon and Losos 2005). Still, niches of species are almost always represented by their mean values in phylogenetic studies (e.g., Luxbacher and Knouft 2009; Kozak and Wiens 2010; but see Evans et al. 2009). Here, we propose a way of incorporating intraspecific niche variability in studies of niche evolution. Instead of retaining the mean niche position and niche breadth over the most important axes, we extracted the scores of all occurrence points on the first two axes yielded by the OMI. For each species, we obtained a bidimensional distribution that can be interpreted as a projection of the climatic niche in the environmental space, maximizing niche differentiation across the whole study group. We used these distributions to resample species' positions along climatic gradients: at each resampling step one, "niche value" on each gradient was randomly selected for each species from its niche distribution on the OMI axes. These values were then used in the phylogenetic analyses. This allowed us to overcome the biases induced by intraspecific niche variability (see the comparison with results without resampling in Appendix S3).

(3) Finally, ancestral state estimation is a step that is traditionally known to generate major uncertainties (Pagel 1997; Losos 1999). After inferring the best model of life-form evolution (see below), we used joint likelihoods of the different life forms for every node in the tree to generate 100 ancestral state reconstructions per tree.

The methods presented below are detailed for one given tree and one set of characters (niche values for extant species and ancestral life forms), but by pooling the results obtained for all resamples of phylogenetic trees, climatic niche positions, and ancestral life forms, we obtained the distributions of all estimated parameters and AIC scores of alternative models. Given that they were not normal, these distributions were always compared using pairwise Wilcoxon signed-rank tests to evaluate if their means were statistically different. All the following analyses have been performed using the R software (R Development Core Team 2011) version 2.12.0 with the *ade4* (Dray and Dufour 2007), *ape* (Paradis et al. 2004), *geiger* (Harmon et al. 2008), *picante* (Kembel et al. 2009), and *diversitree* (FitzJohn et al. 2009) packages.

EVOLUTIONARY HISTORY OF THE CLIMATIC NICHE

As the fragmentation of habitats occupied by *Androsace* could have stimulated niche evolution, we first measured the amount of phylogenetic signal in the climatic niches using two statistics: Blomberg's K (Blomberg et al. 2003; Kembel 2009) and Pagel's λ (Pagel 1999; Freckleton et al. 2002), which differ in their statistical implementation and parameter testing procedures. Using both of them, we prevent ourselves from drawing conclusions from a single method, the potential pitfalls of which have been pointed out (Freckleton et al. 2002; Revell et al. 2008). K compares the distribution of independent contrasts (Felsenstein 1985) to that expected under a Brownian motion (BM) model of trait evolution. Values of K close to 0 imply no signal and values closer or higher than 1 indicate a signal close or greater than expected under a BM model of evolution. K's significance is assessed by data randomization. Pagel's λ is a multiplicative parameter affecting the covariances of characters between different tips of the tree, using a generalized least square optimization. It ranges from 0 to 1, indicating no signal or a signal equivalent to the one expected under BM, respectively. Its significance can be assessed by a likelihood ratio comparison of nested models with particular values (i.e., 0 or 1).

Given the low amount of phylogenetic signal in climatic niches of *Androsace* (see Results), we went a step further and tried to determine how and when niche evolution took place. For this we estimated the tempo and the mode of climatic niche evolution. The tempo describes whether a character has evolved early (close to the root) or late (close to the tips) in a given phylogeny; the mode of evolution discriminates between gradual (i.e., changes

proportional to branch length) and punctual evolution. This was first performed by computing Pagel's δ and κ parameters, which, respectively, measure the tempo and mode of evolution (Pagel 1999; Verdú 2006).

To get a precise view of how niches diversified over time during clade growth and to be able to compare it with the timing of the appearance of the cushion life form, the tempo of niche evolution was also assessed through a disparity analysis (Harmon et al. 2003). Disparity within a clade is calculated here from average pairwise Euclidean distance between species on the two niche axes, and standardized by the disparity of the whole genus. Then, for each speciation event in the phylogeny, the mean disparity is calculated as the average of the disparities of the clades whose ancestral lineage was present at the time of the speciation. By plotting the average subclade disparity against evolutionary time, we obtain a disparity-through-time (DTT) plot, which ranges between 1 (all disparity still to be built) and 0 (all disparity has been accumulated). Observed DTT is then compared to the one expected under a null model of evolution, that is, to BM simulations (10 simulations for each observed DTT). To quantify the results of the disparity analysis, we computed the morphological disparity index (MDI), which compares observed disparity to the one expected under BM (Harmon et al. 2003). Positive values of MDI indicate that disparity is relatively distributed within clades and hence that the trait being studied has evolved relatively recently; alternatively, negative values of MDI are interpreted as evidence of disparity being mainly between clades and of early evolution of the trait (Evans et al. 2009).

EVOLUTION OF LIFE FORMS

Information on species life forms was gathered from the following sources: Flora Helvetica (Lauber and Wagner 2007), Flora Europeae (Tutin et al. 1964+), Flora of China (Hu and Kelso 2007), and Flora of North America (Cholewa and Kelso 2009). Life forms were classified into the three following groups: "short-lived" species for annuals and biannuals, "perennials" for herbaceous perennials, and "cushion" species for long-lived species forming dense mats or cushions, generally displaying woody structures. Using our newly developed phylogeny and by distinguishing cushions from other perennials species, we are extending a previous work on the evolution of life form in *Androsace* that had been performed on a smaller phylogeny (Schneeweiss et al. 2004).

To determine the ancestral life form of the *Androsace* genus and the number of times the cushion life form has evolved, we estimated ancestral life forms over our set of phylogenetic trees using ancestral state reconstructions following the Markov (Mk) model (Lewis 2001) as implemented by Fitzjohn et al. (2009). This was done by fitting and comparing six possible discrete Markov models: a model with all transition rates being different (ARD), the same model but with the tree root constrained to be short-lived (ARD-root), a model with equal transition rates (ER), the same with a short-lived ancestor (ER-root), a model with different rates and transitions between short-lived species and cushions set to zero (NEJ for "No Evolutionary Jumps") and the same with a short-lived ancestor (NEJ-root). Models were compared using AIC. The possibility of having a short-lived ancestor of the genus is highly motivated by the fact that the cushion life form is a derived character in most angiosperm genera (S. Aubert, unpubl. data). Following model selection, we used the best model to run evolutionary simulations of life-form evolution. This was done by drawing histories of life forms from the joint likelihood of each life form on every node of the phylogeny (100 character histories per tree, following Fitzjohn et al. 2009)

RELATION BETWEEN LIFE FORM AND NICHE EVOLUTION

To investigate the role played by life-form transitions in climatic niche evolution and see whether the cushion life form is a key innovation in this genus, we fitted different models of niche evolution to the data, covering a broad range of evolutionary scenarios. We compared a BM model of evolution with various Orstein–Ulhenbeck models (OU, Butler and King 2004). BM models the random walk of niche values; it has been introduced as a model for genetic drift but can also be interpreted as a model of selection in a fluctuating environment, like the one that ancestors of *Androsace* probably experienced. The OU model includes both a random walk and a constraint term. It has been designed to model selection of a continuous character along a phylogeny (Butler and King 2004), with one or several selective optima depending on a priori hypotheses (e.g., Lavergne et al. 2010b). A good fit of an OU model is often interpreted as evidence of evolutionary constraints acting on the character under study. Here, we use OU models to model habitat selection along climatic gradients depending on different possible selective scenarios. The first OU model has a single optimum, common to all current and ancestral species (OU1). In this case, the model assumes that there is a single optimal niche for all the species of the group. The second model (OU2) has two optima depending on well-delimitated clades (Central Asian vs. American–European, see Results), which would imply that different climatic optima have evolved into separate geographic regions, for example due to different specific genetic adaptations of the ancestors of each clade or to climatic differences between the two regions placing different constraints on niche evolution. The last model (OU3) is a model with three optima depending on life form and parameterized with the ancestral reconstructions performed as described above. This last model makes the hypothesis that the three different life forms are suited to different climatic conditions and could indicate that they selected for different optimal climatic tolerances.

Results

PHYLOGENETIC INFERENCE

To date, the phylogeny obtained in this study is the most complete for *Androsace*, including 77 taxa and 72 recognized species of the genus. The topology of the 50% majority-rule consensus tree (Appendix S5) is totally congruent with the results obtained by two complementary works that explored the phylogenetic relationships within *Androsace* and allied genera (Schneeweiss et al. 2004; Wang et al. 2004). Clade supports are, in general, equal or higher to those obtained in these two studies. The ingroup species are divided into two well-supported clades: one constituted by species distributed mainly in Central Asia, the other formed mainly by American and/or European species, and including the nested genera *Douglasia*, *Vitaliana*, and *Pomatosace* (Fig. 1).

Divergence time estimation analyses yielded older age estimates for all nodes (especially deeper ones) than those obtained in previous studies (Schneeweiss et al. 2004; Wang et al. 2004). This is probably due mainly to calibration based on the updated phylogeny of Primulaceae made by Yesson et al. (2009), who obtained a date of 35.4–34.7 Mya instead of the 23 Mya reported by Schneeweiss et al. (2004). The split between the two main clades of *Androsace* s. l. would have occurred 34.9 Mya (95% CI: 34.5–35.3 Mya). The genus *Pomatosace*, sister to the European–American clade, would have diverged 31.9 Mya (95% CI: 28.8–34.2 Mya). In contrast, the two other genera nested within *Androsace*, that is, *Vitaliana* and *Douglasia*, are much more recent: *Vitaliana* would have appeared 1.8 Mya (95% CI: 1.3–8.5 Mya), and the ancestor of *Douglasia* and *A. triflora* Adans. would have diversified 1.5 Mya (95% CI: 0.8–6.6 Mya). Node ages and 95% CI are reported in Appendix S6.

NICHE SEPARATION

The first two axes of the OMI analysis represented 77% of the total inertia of the points included in the study. The first axis (50% of total inertia) correlated negatively with seven (out of eight) precipitation variables, and most strongly with precipitation of the driest quarter and precipitation of the driest month. This first gradient will therefore be referred to hereafter as the "moisture gradient." The second gradient (27% of total inertia) correlated negatively with seven (out of 11) temperature variables and above all with the mean temperature of the coldest quarter, minimal temperature of the coldest month, and mean annual temperature. This second gradient will be referred to hereafter as the "temperature gradient." Although most *Androsace* species could be described as arctic-alpine or alpine species, niche separation was, however, quite significant along these two climatic axis, suggesting that strong niche diversification has occurred in the genus (species scores on the OMI axes shown in Fig. 2).

EVOLUTIONARY HISTORY OF THE NICHE

Although our two estimates of phylogenetic signal were not always convergent, the common pattern was a moderate phylogenetic signal for the niche distributions along the two climatic axes for all sampled phylogenetic trees (Table 1). However, K was never estimated to be greater than 1 and lambda was never close to 1, suggesting a phylogenetic signal lower than the one expected under BM.

On the two environmental axes, δ was always greater than 1 ($\delta = 2.999$ for 99.8% of the resamples on axis 1 and for 99.4% on axis 2, Table 1), thus clearly confirming the expected late diversification of climatic niches. Estimated κ values tend to be quite small for the two axes of the climatic niche (Table 1), indicating that niches have tended to evolve in a punctual way, that is, quite independently of branch lengths. Disparity plots revealed that climatic niches have evolved in a way that is not discernable from BM for most of the evolutionary history of *Androsace* (Fig. 3). This was followed by a fast and marked increase of the niche disparity of climatic niches occurring relatively recently in evolutionary time, with this burst of niche disparification starting approximately around 10 Mya. The MDI obtained across all the resamples was recurrently positive (mean = 0.182, SD = 0.075), suggesting that niche disparity was mostly distributed within subclades and thus confirming the late evolution of climatic niches.

EVOLUTION OF LIFE FORM

The six different discrete Markov models of life-form evolution yielded significantly different AIC values, with the model with the lowest AIC distribution being NEJ-root (Fig. 4A), that is a model with all the rates being different, forbidden transitions between short-lived species and cushions, and the ancestor forced to be short-lived. Rates of transition between perennials and cushions were on average about 10 times higher than rates for the transitions between short-lived species and perennials ($q_{\text{shortlived}\rightarrow\text{perennial}} = 0.023$ Mya^{-1}, $q_{\text{perennial}\rightarrow\text{shortlived}} = 0.0424$ Mya^{-1}, $q_{\text{perennial}\rightarrow\text{cushion}} = 0.541$ Mya^{-1}, $q_{\text{cushion}\rightarrow\text{perennial}} = 0.268$ Mya^{-1}), suggesting that shifts between the short-lived and the perennial life form seldom occurred in the genus. Our results mainly agree with those of Schneeweiss et al. (2004). Reconstructions showed that the cushion life form appeared independently in the two main clades. Hence, we can affirm that it is a homoplasy shared by some Himalayan and some Western (European and North American) species. Only three reversals from perennials toward short-lived species were inferred, whereas Schneeweiss et al. (2004) found at least four. This new result is due to the improvement of the phylogeny, which includes more Central Asian species and thus helps to resolve uncertainties in this clade. We used ancestral life-form reconstructions made using the NEJ-root model for fitting

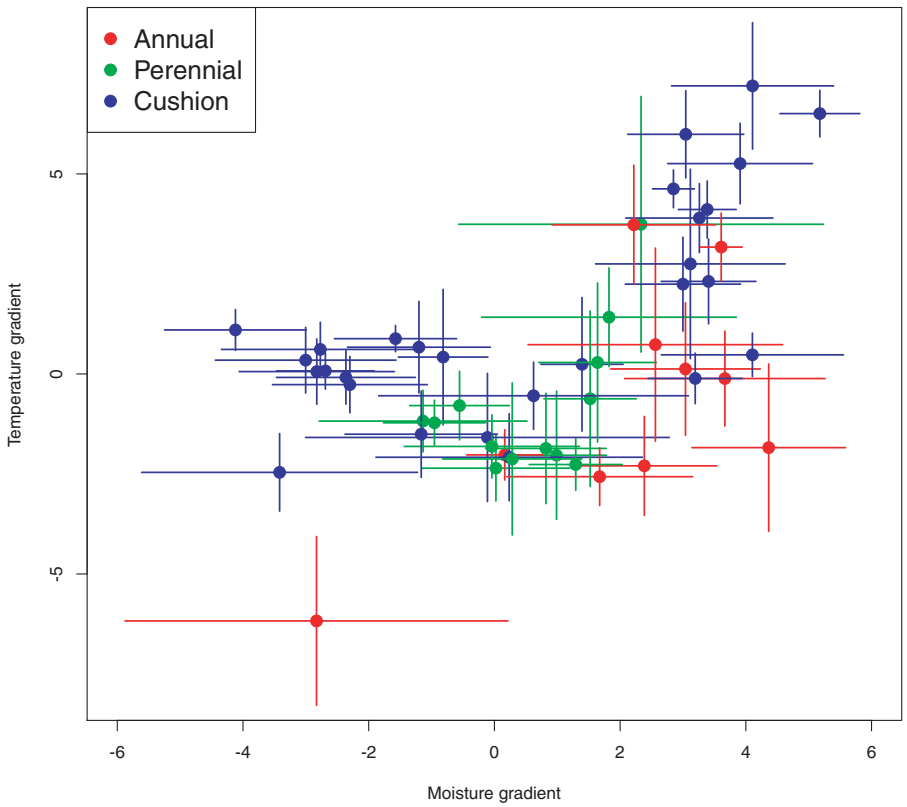

Figure 2. **Climatic niche separation. Ordination plot of mean OMI scores, with standard deviation bars, for 51 species of the *Androsace* genus. Moisture increases and temperature decreases when moving toward higher positive values. Species are colored according to their life forms. Cushions occupy a larger part of the climatic space than other life forms.**

the OU3 model in the following section (marginal likelihoods of the three ancestral states at each node of the phylogeny are shown on Fig. 1).

INFLUENCE OF LIFE FORM ON NICHE EVOLUTION

Different evolutionary scenarios yielded extremely variable AICc distributions, with BM generally yielding the highest AICc values (mean = 523, SD = 20). OU3 had the lowest AICc values (mean = 485, SD = 15), and was therefore the model that best described niche evolution among the models we compared (Fig. 4B). Climatic optima estimated for different life forms and across all trees, drawn niche values and ancestral state reconstructions showed that short-lived species displayed the driest climatic optimum, and that the coldest temperature optimum was for cushion species (Fig. 5).

Discussion

One of the main arguments supporting the importance of niche conservatism is that most clades generally occupy only one or a few given biomes (e.g., Crisp et al. 2009 for plants). This observation leads to the conclusion that adaptations to new climates have often been difficult (Donoghue 2008), carrying important implications for the future distribution of species in the face of climate change. However, a few biological groups have managed to colonize extreme environments over relatively short timescales, thus challenging common wisdom about niche conservatism. The macroevolutionary study of such groups is therefore necessary to reveal the general mechanisms that enable adaptation to changing environments. Our study of niche and trait evolution in *Androsace* provides one of these much-needed examples.

Table 1. **Estimated indices of phylogenetic signal, tempo, and mode of evolution. For each index used, the mean (± standard deviation) of all values obtained over the 10,000 resamples is presented for each OMI axis. The two exponents indicate the percentage of *P*-values ≤ 0.05 in the tests against the particular values of 0 and 1, respectively (*K* is only tested against 0). Note that δ stops at 2.99 due to its calculation in the geiger package in R.**

	K	λ	δ	κ
OMI 1	$0.29\ (\pm 0.08)^{85-}$	$0.63\ (\pm 0.21)^{83\,92}$	$2.99\ (\pm 0.02)^{100\,100}$	$0.21\ (\pm 0.19)^{100\,100}$
OMI 2	$0.29\ (\pm 0.09)^{72-}$	$0.64\ (\pm 0.20)^{68\,90}$	$2.99\ (\pm 0.05)^{100\,100}$	$0.16\ (\pm 0.16)^{100\,100}$

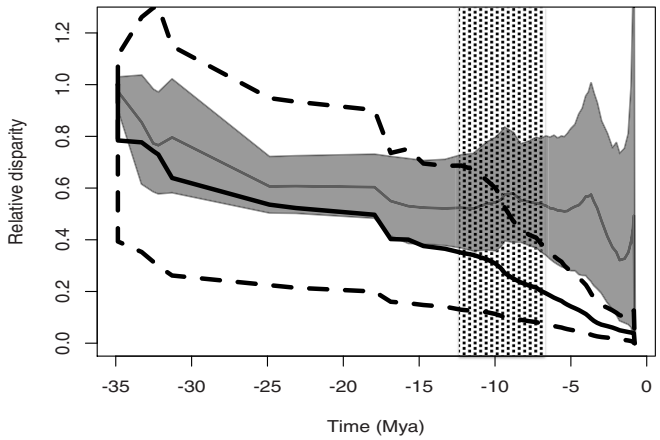

Figure 3. **Relative disparity through time (DTT) for the climatic niche in *Androsace*. In black, the bold and dashed lines indicate, respectively, the mean and the 5% and 95% quantiles of the Brownian Motion simulations (10 simulations for each resampling step). The bold line in gray and the shaded area indicate the mean and 95% envelope of the observed disparities in the 10,000 resamples taken from niches and trees. As trees have different branching times, all curves are plotted against the mean time of each speciation event across the 100 trees. The dashed area indicates the approximate period between the two appearances of the cushion life form, probably in Asia (−12.5 ± 2.8 Mya) and in Europe (−7.4 ± 2.6 Mya), which seems to coincide with the increase in disparity.**

NICHE LABILITY IN ANDROSACE

This study reveals significant evolutionary lability of climatic niches in the *Androsace* genus, as indicated by a weak phylogenetic signal and strong interspecific disparity in climatic optima along temperature and moisture gradients. Although most *Androsace* species tend to occur in relatively cold environments, niche separation illustrates clear differences between their climatic requirements. For example, the mean annual temperature in the genus ranges from −10.4°C for *Douglasia ochotensis* to 18.4°C for *A. umbellata*, European species occupying slightly wetter and warmer environments than American or Central Asian ones (Appendix S1). Dimensions of niche differentiation vary between the two main *Androsace* clades. In the Central Asian clade, species' niches are primarily distinguished along the temperature gradient. For example, *A. umbellata*, found in New Guinea, has the warmest niche position and shows almost no niche overlap with other *Androsace* species. Within the American–European clade, niche differentiation is mainly driven by the moisture gradient, which is due to the Rocky Mountains or Alaska regions being relatively drier than European mountain ranges. Phylogenetic comparative analyses of climatic niches in the *Androsace* genus reveal the reasons for this lability. Indeed, the recent diversification of species' niches (high values of δ and positive MDI) through punctual evolution (low values of κ) is likely to have erased most of the phylogenetic legacy in species environmental requirements,

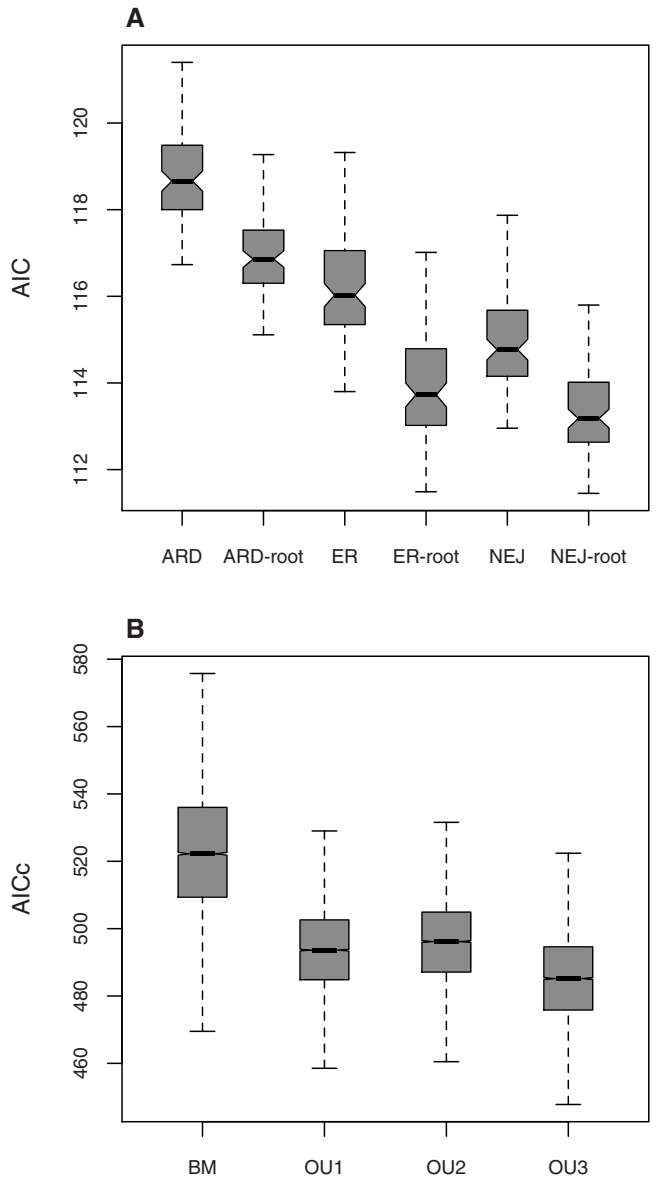

Figure 4. **Evolutionary models comparisons. (A) AIC distributions of the six Mk models fitted on the 100 trees with 62 species. (B) AICc distributions of the four niche evolution models, fitted for 51 species on 10,000 resamples from trees, niches, and ancestral life forms where necessary. All AIC and AICc distributions are significantly different according to Wilcoxon signed-rank tests (all *P*-values < 0.01).**

resulting in low phylogenetic signal. We can conclude that the climatic niches of *Androsace* have not been conserved through evolutionary time but instead underwent a late and rapid radiation.

These findings are in agreement with the prediction that isolation of lineages leads to niche evolution (Ackerly 2003; Donoghue 2008). Indeed, the orogeny of the Alpide belt (the mountain range that extends along the southern margin of Eurasia, from the Pyrenees to New Guinea) started around 40 Mya (Nikonov 1988) and proceeded at high rates until the present day, leading to the

sharp topography we observe today (Hergarten et al. 2010). Ancestral lineages of *Androsace* probably rode this mountain uplift, thus becoming progressively isolated from each other by eroded valleys (Kuhlemann 2007) and lowlands. The lack of zoochory opportunities for plants that do not produce fleshy fruits and the absence of seed adaptation to long distance dispersal (as noted in *A. alpina* by Schonswetter et al. 2003) may have increased this geographic isolation. In addition, Cenozoic Era climatic and glacial oscillations (Zachos et al. 2008) are likely to have alternately opened pathways between populations and created environmental barriers between favorable regions. The punctual evolution of the climatic niche we observed in *Androsace* could be the result of colonization events enabled by the opening of these pathways during colder periods, followed by speciation and rapid adaptation after isolation. Numerous cases of rapid niche disparification in plant lineages following colonization of island-like habitats have already been documented. Perhaps the most striking cases are those of the Hawaiian silverswords (Witter and Carr 1988 Evolution) and of the Andean species of the genus *Lupinus* (Hughes et al. 2006), both displaying tremendous variation in life form (from weeds of a few centimeters to trees) and habitat. The case of *Androsace* is however different because it has less variation in life form and habitat but higher variation in climatic tolerances.

THE RISE OF THE CUSHION LIFE FORM

Interestingly, the diversification of climatic niches observed in *Androsace* has been enhanced by life-form evolution. Short-lived *Androsace* tend to occupy the driest niches (e.g., dry steppes and plains), which is consistent with previous observations that seed dormancy of annual plants prevents local extinction during drought periods (Körner 1999), even in dry alpine regions (e.g., the central Chilean Andes, Arroyo et al. 1999). The fact that the coldest environments are occupied by cushion *Androsace* corroborates eco-physiological evidence that the cushion's dense canopy acts as a temperature variation buffer by elevating the temperature inside the plant (Körner 1999; Larcher et al. 2010), thus enabling tolerance to colder conditions.

Our study reveals that the ancestor of *Androsace* was a short-lived species, probably therefore inhabiting cold steppes in Eurasia. The cushion life form then appeared independently in the two main clades, as they were already geographically isolated in Asia and Europe (Schneeweiss et al. 2004). These two events occurred roughly around 12.5 Mya in Asia and 7.4 Mya in Europe (see Fig. 1, nodes 24 and 57 are shown in Appendix S5 and dated in Appendix S6). Similar cases of repeated evolution of a morphological trait in a clade have already been studied and can be explained by similar selection pressures in geographically isolated environments (Wiens et al. 2006). Even if our large-scale approach cannot directly demonstrate it, the convergent evolution of the cushion life form in the Central Asian and American–European clades could be attributed to strong selection pressures toward cold tolerance resulting from the rapid rise of the Alpide belt in the Miocene and to similar biotic contexts (i.e., temperate biomes of the Northern Hemisphere, Fine and Ree 2006).

THE CUSHION LIFE FORM: A KEY INNOVATION

Although a macroevolutionary study such as ours does not enable the investigation of the precise mechanisms by which plant morphological adaptations permit particular climatic tolerances, we can suggest from our results that the evolution toward harsh alpine niches has been enabled by the emergence of the cushion life form. Indeed, the fact that a model with several selective optima (OU3) has a better fit than a model of drift (BM) model indicates that different climatic constraints have acted on the different life forms. This result is even stronger when we note that the ancestors of *Androsace* have probably experienced a fluctuating environment, a situation ideally modeled by BM. Therefore, the selection toward optimal niches in each life form has been strong enough to overcome the effects of climate fluctuations. We can consequently affirm that the cushion life form is a key innovation in the genus *Androsace*, leading to a significant change in the fundamental niche of the species that possessed it and allowing them to colonize the cold habitats created by the alpide orogeny. Key innovations are known to be major sources of ecological opportunity and are often associated with increased niche disparity (Losos and Mahler 2010). Even if our study does not specifically address this question, it can provide a qualitative answer to it. Indeed, the fast increase of niche disparity found here seems to coincide with the emergence of the cushion life form (Fig. 3), even if we did not specifically tested that this increase was mainly due to clades possessing the cushion life form. Moreover, cushions seem to have a broader occupancy of the climatic space than other life forms (Fig. 2). Further work is still needed to see whether cushions also stimulated diversification rates, a consequence that would be expected from such a key innovation (Glor 2010) and that has already been observed in many lineages that colonized the Andes (Donoghue 2008).

A GENERAL SCENARIO FOR THE EVOLUTION OF ALPINE PLANTS?

Putting together our results gives a clear picture of the evolution of cold tolerance in *Androsace*, which can be summarized in the following scenario. Ancestors of the genus, probably already adapted to the temperate conditions of cold steppes, rode the rising mountain chain of the Alpide belt. The increasing isolation of these new "continental islands" combined with poor dispersal ability prevented species from migrating back to their optimal habitats and instead forced them to adapt in situ to survive. Under the strong selection pressures for increased cold tolerance that these species experienced, the cushion life form evolved as a

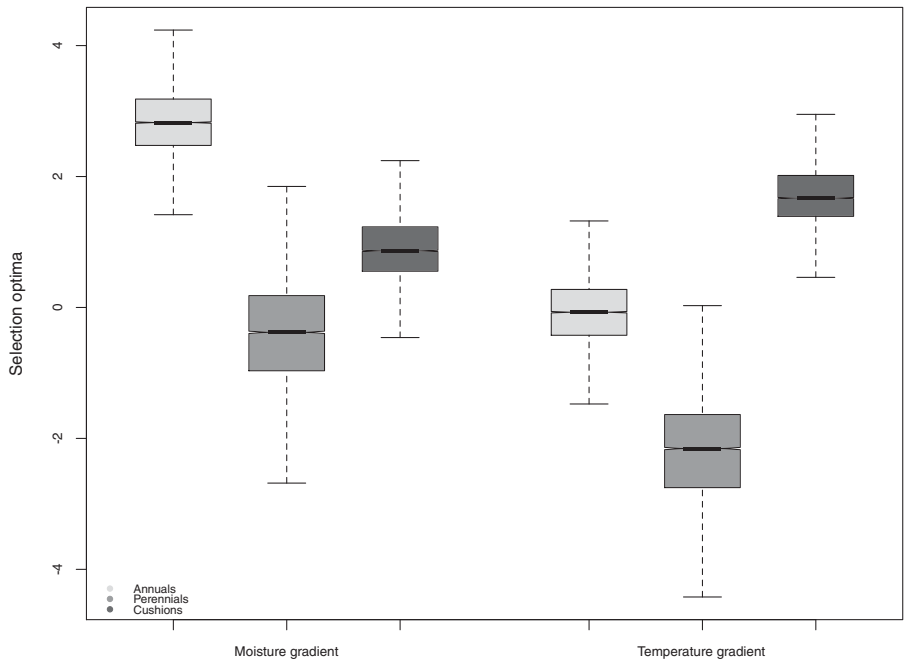

Figure 5. Estimation of the niche evolutionary optima for the OU3 model on the two main environmental gradients, for the three different life forms. All optima distributions are significantly different according to Wilcoxon signed-rank tests (all *P*-values < 0.01). The driest niches have been selected in short-lived species and the coldest in cushions.

key morphological innovation, enabling the occupation of novel alpine habitats.

This scenario is strikingly similar to the one inferred for the evolution of *Espeletia* (Asteraceae) by Monasterio and Sarmiento (1991). This Andean plant genus originated as a rainforest tree and subsequently colonized the high-altitude paramo habitats created by the Andean orogeny due to the evolution of the pachycaulous life form. The similar environmental conditions and orogenic history along with the presence of the same pachycaulous morphology in several genera of tropical-alpine plants such as *Puya* in the Andes and *Dendrosenecio* and *Lobelia* in East Africa suggest that their evolutionary history could have been similar. Despite differences between climatic conditions in tropical highlands and cold areas of the Northern Hemisphere (Körner 2007), the scenario proposed above may quite effectively describe the general stages for the evolution of adaptation to alpine habitats in plants. Several plant genera distributed in the Holarctic ecozone and that contain species bearing the cushion life form such as *Saxifraga*, *Draba*, or *Silene* would be preferred candidates to test the generality of this scenario.

ASSUMPTIONS AND POSSIBLE SOURCES OF ERROR

Our study potentially presents some limitations. First, there is a strong disequilibrium between Central Asian and American–European species, the former being sampled a lot less (in terms of the occurrence points as well as for the phylogeny). However, the analysis conducted on a subset of species with at least 15 points (a number that has been demonstrated to be large enough for a reliable niche estimation, Stockwell and Peterson 2002) shows the robustness of our results (Appendix S2) and the low fit of the OU2 model compared to OU3 also indicates that climatic differences between clades are not as important as differences explained by biological traits. Second, we used climate data obtained by large-scale interpolations and thus containing potential errors. It is hoped that the resampling procedure we applied on the niche distributions helped to alleviate the effects of these errors. We must also recognize that as in all attempts to incorporate climatic variables in studies of macroevolution, we cannot rule out that climatic variables were differently correlated in the past. As already mentioned, soil ecology is known to be an important driver of alpine plants distributions (Alvarez et al. 2009) and could be a confounding factor in our work. This variable was anyway not available at such a large geographic scale and we believe moreover that this large scale prevents soil type from being totally confounded with one climatic variable. Lastly, it is important to stress that microevolutionary experiments on the selective advantage of different life forms in different environmental conditions would really help to corroborate our speculation concerning the parallel evolution of cushions and alpine niches.

Conclusion

In a recent debate on the niche conservatism paradigm, some authors (e.g., Losos 2008b) suggested that more studies on

different groups were necessary to assess the generality of this phenomenon. Moving away from the extensively studied examples of groups of reptiles and amphibians, we provide, through comprehensive analysis, a robust and clear answer for a genus of arctic-alpine plants in which niche lability prevails. As noted by some authors (e.g., Wiens 2008; Cooper et al. 2010), raw estimations of phylogenetic signal are of little interest when attempting to understand niche evolution. Including simple measures such as the tempo and mode of evolution of the niche, as well as a biological trait, enables us to better understand niche evolution in a particular group, making the link between ecology and evolution clearer. In doing so, we showed how occupation of alpine niches in *Androsace* has been triggered by the emergence of a key innovation: the cushion life form.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. List of all taxa included in the study, showing all GenBank IDs.

Appendix S2. Sensitivity analysis.

Appendix S3. Utility of the resampling procedure.

Appendix S4. Overall workflow of the comparative study.

Appendix S5. Chronogram based on Bayesian 50% majority-rule consensus tree.

Appendix S6. Node ages estimated for the Bayesian 50% majority-rule consensus tree, standard deviation (SD), and 95% confidence interval (95% CI) for each node.

Supporting Information may be found in the online version of this article.

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ARTICLE 3.2

RADIATIONS REPLIQUEES DANS LE GENRE *ANDROSACE* : ROLE DE L'EXPANSION GEOGRAPHIQUE ET CONVERGENCE VERS LA MEME INNOVATION CLEF

Journal of Biogeography (J. Biogeogr.) (2013)

ORIGINAL ARTICLE

Replicated radiations of the alpine genus *Androsace* (Primulaceae) driven by range expansion and convergent key innovations

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ABSTRACT

Aim We still have limited understanding of the contingent and deterministic factors that have fostered the evolutionary success of some species lineages over others. We investigated how the interplay of intercontinental migration and key innovations promoted diversification of the genus *Androsace*.

Location Mountain ranges and cold steppes of the Northern Hemisphere.

Methods We reconstructed ancestral biogeographical ranges at regional and continental scales by means of a dispersal–extinction–cladogenesis analysis using dated Bayesian phylogenies and contrasting two migration scenarios. Based on diversification analyses under two frameworks, we tested the influence of life form on speciation rates and whether diversification has been diversity-dependent.

Results We found that three radiations occurred in this genus, at different periods and on different continents, and that life form played a critical role in the history of *Androsace*. Short-lived ancestors first facilitated the expansion of the genus' range from Asia to Europe, while cushions, which appeared independently in Asia and Europe, enhanced species diversification in alpine regions. One long-distance dispersal event from Europe to North America led to the diversification of the nested genus *Douglasia*. We found support for a model in which speciation of the North American–European clade is diversity-dependent and close to its carrying capacity, and that the diversification dynamics of the North American subclade are uncoupled from this and follow a pure birth process.

Main conclusions The contingency of past biogeographical connections combined with the evolutionary determinism of convergent key innovations may have led to replicated radiations of *Androsace* in three mountain regions of the world. The repeated emergence of the cushion life form was a convergent key innovation that fostered radiation into alpine habitats. Given the large ecological similarity of *Androsace* species, allopatry may have been the main mode of speciation.

Keywords

Allopatry, *Androsace*, biogeography, cushion plants, diversification, evolutionary determinism, historical contingency, long-distance dispersal, speciation rates.

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INTRODUCTION

Discerning the processes that foster species diversification and shape spatial patterns of biodiversity is a major challenge in evolutionary biology (Schluter, 2000). Although recent studies have reported exceptional species radiations (e.g. Hughes & Eastwood, 2006; Valente *et al.*, 2010), little is known about the driving forces of the evolutionary success (i.e. higher speciation rates and geographical expansion; Gould & Eldredge, 1977) of some clades while close relatives

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remain species-poor or geographically restricted. In particular, the relative influence of historical contingency (i.e. stochastic past events) versus deterministic processes (i.e. similar selective pressures leading to convergent evolution) in driving species radiations remains unclear (Schluter, 2000; Losos & Mahler, 2010). Evidence for the prevalence of determinism in nature is provided by the increasing number of replicated adaptive radiations and evolutionary convergences documented in various groups of plants and animals (Schluter, 2000; Vermeij, 2006). In such cases, different clades facing similar environmental conditions developed convergent key innovations, which provided the stimulus for increased species and niche diversification, e.g. toe pads in lizards (Larson & Losos, 1996), phytophagy in insects (Farrell, 1998), and pharyngeal jaws in fish (Mabuchi *et al.*, 2007). However, rare events that have given rise to unprecedented ecological opportunities have been highlighted to show the importance of historical contingencies on organism diversification (Losos & Mahler, 2010). The most common type of contingent event might be long-distance dispersal (hereafter, LDD) (Nathan, 2006; Gillespie *et al.*, 2012), a phenomenon best exemplified by organisms that have colonized remote oceanic islands and radiated *in situ* (e.g. Hawaiian violets; Ballard & Sytsma, 2000).

In comparison to islands, which have traditionally served as natural laboratories for evolutionary studies (Losos & Ricklefs, 2009), less is known about the history of continental clades because of their complex geographical and historical settings. However, some continental systems exhibit a certain degree of similarity with island systems in that they are delimited to identifiable and distinct geographical units. Among such systems, mountain ranges constitute networks of cold environmental islands (Ackerly, 2003) that can be seen as continental analogies of island archipelagos systems (Gehrke & Linder, 2009). Like oceanic islands that have different ages, mountain ranges with their own specific orogenic histories allow us to compare the tempo of species diversification of sister lineages. Recent studies on tropical mountain taxa have enhanced our understanding of adaptive radiations (e.g. Hughes & Eastwood, 2006; Särkinen *et al.*, 2011). However, examples of evolutionary radiations in temperate mountain ranges are quite scarce (but see Emadzade & Hörandl, 2011), probably due to the fact that the extreme abiotic conditions in these regions led to lower rates of diversification than energy-rich environments.

Here, we attempt to understand the evolutionary success of rock-jasmines, i.e. the plant genus *Androsace* s.l. (*sensu* Martins *et al.*, 2003). The case of *Androsace* is intriguing for two main reasons. First, the genus has successfully colonized most temperate and arctic–alpine regions of the Northern Hemisphere although it is mainly made up of narrow endemics with low dispersal abilities (Anderberg & Kelso, 1996). Second, *Androsace* species seem to have diversified in three major regions (Central Asia, Western Europe and Northern America) reaching a relatively high number of species within the genus (*c.* 110 species), most of them found in alpine habitats (see Fig. S1 in Appendix S1 in Supporting Information). This is somehow unexpected given the general observation that arctic–alpine ecosystems are species-poor (McCain & Grytnes, 2010) and have low productivity (Körner, 1999), which may limit the opportunities for diversification (e.g. O'Brien, 1998; Francis & Currie, 2003). *Androsace* displays a variety of life forms including annual, herbaceous perennials and cushions, i.e. slow-growing plants in compact form with very dense leaf canopy, characterized by extremely long individual lifetimes. Recently, Boucher *et al.* (2012) demonstrated that the cushion life form evolved independently in two separate clades as a key innovation that led to the occupancy of the extremely cold 'alpine niches'. What remains puzzling and unexplored is how the genus *Androsace* has colonized most of the Northern Hemisphere, and which processes led to the pattern of increased species richness in alpine regions. In particular, it remains unknown whether the cushion life form fostered diversification in the genus and whether ecological forces have been regulating cladogenesis in different geographical areas.

Here, we address several questions raised by previous studies on *Androsace*. We explore how the various life forms, which have different climatic tolerances, longevities and dispersal abilities (due to variable seed weight) may have triggered the geographical spread and diversification of *Androsace* in different ways. To answer this, we analysed a comprehensive data set including geographical distributions, climatic preferences, morphological data and phylogenetic relationships for nearly two-thirds of all *Androsace* species. We reconstructed the historical biogeography of the genus and defined the most likely migration routes across the mountain ranges of the Northern Hemisphere. We then examined the tempo of diversification in three main geographical regions (Central Asia, Europe and North America) and tested the relative role of the cushion life form and climatic niche vicariance (i.e. divergence of sister species due to specialization to different climatic regimes) in the diversification of *Androsace*.

MATERIALS AND METHODS

Study group

Androsace s.l. comprises the (former) genera *Androsace*, *Douglasia*, *Pomatosace* and *Vitaliana* (Martins *et al.*, 2003; Schneeweiss *et al.*, 2004). Its highest species richness is located in the Himalayas and Hengduan Mountains (a plant endemism hotspot in Western China; López-Pujol *et al.*, 2011). The three life forms found in *Androsace* tend to occupy different habitats: short-lived species (annual or biennial) mainly occur in cold steppes, rosette perennials occupy mesic subalpine and alpine meadows or open woodlands, and cushion species occur on alpine scree slopes or cliffs, sometimes at very high elevations (up to 3850 m in the French Alps; S. Lavergne, Laboratoire d'Écologie Alpine, pers. comm.). Cushions occupy the coldest niches; annuals and

perennials are adapted to the driest and wettest environments, respectively (Boucher *et al.*, 2012). Despite life-form differences, *Androsace* species have similar floral morphology, with relatively large white or pink homostylous flowers (except for *Vitaliana primuliflora* Bertol., which produces yellow, heterostylous flowers).

Biogeographical inference

Different life forms may have had varied importance in the geographical spread of the genus. Migration could have been fostered by annuals because of their lighter seeds and wider climatic tolerances. We tested two alternative biogeographical scenarios with the dispersal–extinction–cladogenesis (DEC) parametric method implemented in Lagrange (Ree & Smith, 2008), which is able to integrate temporal and dispersal inputs. This enables the comparison of biogeographical hypotheses based on their likelihood. As Lagrange takes branch lengths of the provided phylogeny into account and allows us to define the specific dispersal probabilities between geographical areas, this program enables the integration of temporal and dispersal variables into the comparison of alternative biogeographical hypotheses using likelihood.

Biogeographical analyses were conducted on two spatial scales: continental and regional. At a continental level, we looked for broad patterns in the biogeographical reconstruction and tested which area delimitation (see Fig. 1, and Fig. S2 in Appendix S1) best suited *Androsace* species. At a regional level, we defined the following areas for which two or more species were endemic: (A) Iberian Peninsula (excluding the Pyrenees); (B) Pyrenees; (C) Alps and Apennines; (D) south-eastern Europe; (E) Caucasus; (G) Himalayas; (H) Tibetan Plateau; (F) Hengduan Mountains; (J) Eastern Asia region; (I) Asian Arctic region and Mongolian plateau; (M) North American Arctic region; (K) Cascade Range; (L) Central Rocky Mountains and Central North America (Fig. 2).

Two biogeographical models were then compared at a regional level – a baseline model without dispersal constraints, and a stepping-stone model with higher dispersal probabilities between neighbouring areas than between non-neighbouring ones (Fig. S3 in Appendix S1). Neighbouring areas were defined as adjacent areas or areas that do not have another area or sea between them that could act as a barrier (except for Arctic Asia and Arctic North America, which were considered as neighbouring areas due to the lability of the Bering Strait; Hopkins, 1967; Wen, 1999). We also constrained the number of maximum areas of ancestral range to see whether this led to a better model.

All biogeographical analyses were run for 100 phylogenetic trees from Boucher *et al.* (2012). The phylogenetic trees included 72 species of the study group, thus covering nearly two-thirds of *Androsace* species (*c.* 110). These phylogenies were based on two DNA regions (ITS and *trn*L–F) and were built using Bayesian inference on MrBayes (Ronquist & Huelsenbeck, 2003), and run over 20 million generations, sampling one tree every 100 steps. A random set of 100 phylogenies from the posterior distribution of trees were dated with a Bayesian relaxed molecular clock (Yang, 1997; Kishino *et al.*, 2001; Thorne & Kishino, 2002), which was calibrated with the divergence time range estimations of the *Androsace* lineage obtained by Yesson *et al.* (2009). Ancestral area reconstructions for each node were averaged in a consensus tree. When several reconstructions were obtained for a given node, they were weighted by their marginal probability at this given node. To summarize the results for each node (pie charts in Figs 1–2), only the trees where the node was present were used, thus yielding a 'node-by-node reconstruction' (Nylander *et al.*, 2008).

Diversification analyses

The cushion life form has been identified as a key morphological innovation in *Androsace* that facilitated the occupation of colder alpine environments (Boucher *et al.*, 2012). Macro-evolutionary theory predicts that this new life form would have increased diversification rates (either increasing speciation or decreasing extinction rates) due to the ecological opportunity it provided (Glor, 2010; Yoder *et al.*, 2010). To test this prediction, we used the MuSSE (Multiple State Speciation Extinction) framework (Fitzjohn *et al.*, 2009), which accounts for different rates of speciation and/or extinction depending on the state of a discrete trait, while simultaneously estimating the ancestral states of this trait using a likelihood approach. Life forms of extant species were classified into three categories – short-lived (annuals, biennials), perennials and cushions (see Boucher *et al.*, 2012). Diversification methods that can deal with incomplete phylogenies require random undersampling, which was not the case here (all European and North American species are included, but only half of the Asian ones). Thus, we defined two monophyletic clades with a coherent geographical distribution and ran the analyses independently on both of them: the (mainly) Central Asian clade (Fig. 1); and the clade formed by 32 species distributed in Europe and North America (stemming from node B; see Fig. 1; hereafter 'North American–European clade'). Four models of diversification were used: (1) a pure birth model with a single speciation rate (PB); (2) a birth–death model common to all species (BD); (3) a model with different speciation and extinction rates for each life form (BD-Form); and (4) a model with different speciation rates but null extinction for each life form (PB-Form). Given that a previous study showed that the ancestor of *Androsace* species was probably short-lived, and that it is very unlikely that short-lived species could directly evolve into cushion species (Boucher *et al.*, 2012), we defined the root of the tree as short-lived in each clade and we did not allow any evolutionary jumps from short-lived to cushions. For the Central Asian clade, sampling was fixed at 57% of short-lived species, 25% of perennials and 44% of cushions, according to taxonomic knowledge (Nasir, 1984; Hu & Kelso, 1996).

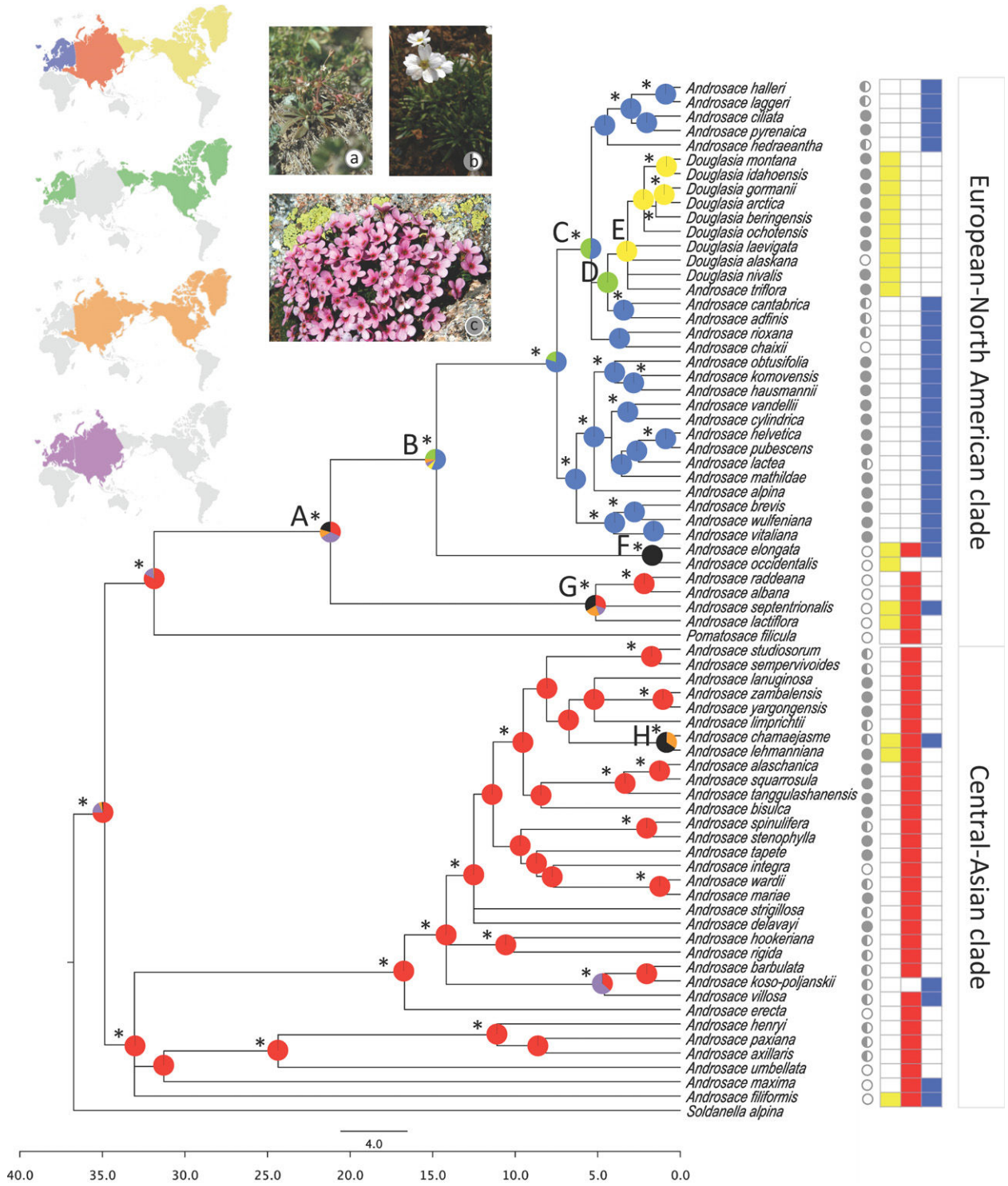

Figure 1 Continental-scale biogeographical reconstruction plotted on the *Androsace* consensus tree. The time-scale at the bottom is in millions of years. World maps show the three areas defined for the continental analysis and all their possible combinations. Pie charts represent the relative probability of ancestral area reconstructed for each node averaged over the 100 trees, with colours corresponding to the areas highlighted on the world maps. Asterisks indicate nodes with a posterior probability ≥ 0.95. Black portions represent ancestral reconstructions spread on the three defined areas. On the right side of tip labels, circles indicate species' life forms: grey circles represent cushions; half-filled circles indicate perennials; and empty circles are short-lived species. These three life forms are illustrated with one photograph each: (a) *A. elongata* L., annual (photo: S. Aubert/SAJF); (b) *A. lactea* L., perennial (photo: S. Aubert/SAJF); (c) *A. laggeri* Huet, cushion (photo: C. Roquet). Coloured boxes on the extreme right show current geographical distributions corresponding to the distribution map. Some nodes are labelled with a letter for text discussion.

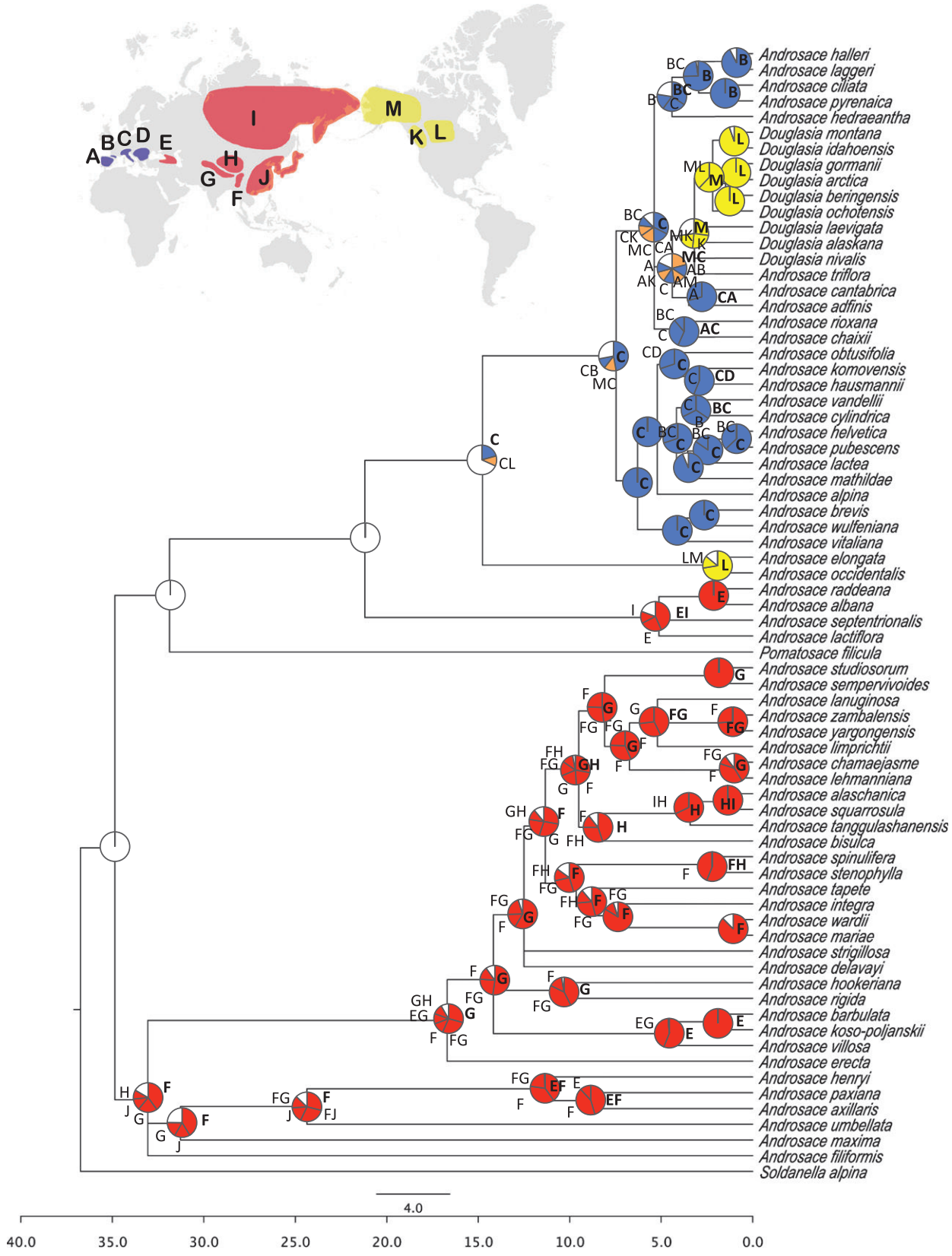

Figure 2 Regional-scale biogeographical reconstruction plotted on the *Androsace* consensus tree. Pie charts represent the relative probability of ancestral area reconstructed for each node averaged over the 100 trees. Letters next to pie charts correspond to areas of distribution with codes as in the world map; bold letters correspond to the portion with a highest probability. Colours of the pie chart portions correspond to continental-scale areas as in Fig. 1; white portions represent reconstructions with a probability < 0.10.

Examining the tempo of diversification in a clade can provide insights into potential ecological regulation of cladogenesis. Declining diversification rates over time may suggest that a diversity limit was reached during diversification (Rabosky, 2009). Density-dependent diversification can be explicitly modelled using a logistic growth function for speciation rates and a clade's upper diversity bound can be estimated (Rabosky & Lovette, 2008). This limit is frequently thought to be the result of niche partitioning between interacting members of the clade and is one of the main signatures of adaptive radiations (Losos & Mahler, 2010). However, such diversity limits could also arise as a consequence of decreasing range sizes following successive events of allopatric speciation (Rosenzweig, 1996). In the case of *Androsace*, the clades found in Central Asia, Europe and Northern America may be at different stages of diversification, because they have different ages and geographical contexts. To determine whether each of these clades has reached a diversity bound, we used the likelihood framework for density-dependent diversification implemented in the R package DDD (Etienne & Haegeman, 2012). In order to meet the hypothesis of random undersampling, we first analysed the Central Asian clade on its own by fitting four different models: (1) a pure birth model (PB); (2) a birth–death model (BD); (3) a density-dependent model with no extinction (DDL); and (4) a density-dependent model with extinction (DDL+E). We applied the same four models to the North American–European clade, and also tested the hypothesis that North American species underwent their own diversity dynamics by enabling a decoupling of the diversification of the North American subclade (stemming from node E, Fig. 1) versus the main clade (Etienne & Haegeman, 2012). This resulted in four additional models being fitted: (5) a model where European species experience density-dependence with no extinction but North American species follow a pure birth process (DDL/PB); (6) the same model with extinction in both clades (DDL+E/BD); (7) a model where both European and North American species experience density-dependence with no extinction but at different paces and with different carrying capacities (DDL/DDL); and finally (8) the same model with extinction (DDL+E/DDL+E).

All diversification analyses were run on 100 phylogenetic trees and alternative models were compared using the Akaike information criterion (AIC). In all density-dependent diversification models, the speciation rate was assumed to depend linearly on species richness, and the last 0.6 Myr (during which no branching occurs) were chopped off to avoid detecting a final negative rate shift due to a lack of species recognition (i.e. incipient species not detected in the phylogeny because of incomplete speciation; Egan & Crandall, 2008). Models without extinction were specified by fixing the extinction rate to zero, and models without density-dependence in the subclade (i.e. DDL/PB and DDL+E/BD) were approximated by giving a very large value to the carrying capacity ($K = 5000$).

Androsace species show low levels of sympatry and species belonging to the same life form are usually found in similar habitats. Thus, parapatric speciation due to climatic vicariance is unlikely. However, in order to discard the hypothesis that climatic vicariance may have played an important role in speciation events of *Androsace*, we performed a set of statistical analyses implemented in the software SEEVA (Struwe *et al.*, 2011), and this showed that climatic vicariance played no role in the speciation of the genus. See Appendix S1 for a detailed description of the analyses performed and Appendix S2 for the results.

RESULTS

Biogeographical reconstruction

The continental and regional analyses led to congruent results for the main biogeographical patterns (Figs 1–2). At a continental level, the area delimitations with the highest likelihood were: (a) Europe; (b) North America and Arctic Asia; and (c) Asia excluding the Arctic (see Table S1 in Appendix S2). In the regional analyses, the stepping-stone model yielded a higher likelihood than the baseline model (Fig. S4 in Appendix S2). Restricting the ancestral range to two areas also gave higher likelihood values, which was congruent with the distribution range of most *Androsace* species, with most of them being restricted to one or two areas. Hence, we will only present the results obtained with these settings here.

The continental analysis suggested an Asian ancestor for *Androsace* (Fig. 1), followed by at least two LDD events: first, to Europe in the early–middle Miocene (nodes A and B; Fig. 1); secondly, to North America in the late Miocene–Pliocene (nodes C and D; Fig. 1). In addition, there were intercontinental dispersal events for three minor clades: (1) from Asia to other continents by the ancestor of *A. chamaejasme* Wulfen (Holarctic distribution) and *A. lehmanniana* Spreng. (present in Alaska and Asia); (2) from Asia to Europe by the ancestor of *A. villosa* L. (widespread in the mountains of Europe and Western Asia) and two western Asiatic species, *A. barbulata* Ovcz. and *A. koso-poljanskii* Ovcz.; and (3) from Europe to other continents by the ancestor of the North American endemic *A. occidentalis* Pursh and the widespread *A. elongata* L.

Results for the regional analyses suggested that the ancestors of most of European species originated from the Alps and Apennines, and subsequently expanded to the Pyrenees and south-eastern Europe mountain areas. Results for *Douglasia* and *A. triflora* Adans. (nested within *Douglasia*) showed an ancestor from the south-western European mountains that spread to North America through LDD. In the Asian clade, a high proportion of ancestors were distributed in the Himalayas and/or the Hengduan Range.

Diversification analysis

When trying to determine the influence of life forms on the diversification in *Androsace*, the model that fitted best in both clades was the PB-Form model where speciation

Table 1 Speciation rates (species per million years) estimated in the two main clades of *Androsace* using a pure birth model with different speciation rates but null extinction for the three life forms (PB-Form). Means and standard deviations over the 100 trees are presented.

	Short-lived	Perennial	Cushions
Central Asian clade	0.037 ± 0.0003	0.140 ± 0.0212	0.282 ± 0.018
North American–European clade	0.052 ± 0.002	0.183 ± 0.0778	0.216 ± 0.0282

rates were different for each life form but extinction was null (mean $\Delta AIC > 5.2$ with all other models and in the two clades; see Table S3 in Appendix S2). Lineages with a cushion life form experienced significantly higher speciation rates than the other life forms in both clades (Table 1).

However, contrasting diversification patterns were found for different clades. All models had similar AIC scores in the Central Asian clade, but a pure birth model was slightly favoured over the others (Table 2). The constant speciation rate was estimated to be 0.124 ± 0.004 species Myr^{-1}. A decoupling of diversity dynamics was detected in the North American–European clade, where the most likely model suggested diversity-dependent diversification in Europe and pure birth process in North America (Table 2; see also the lineage-through-time plot Fig. 3). In this model, European species experience diversity-dependence with an estimated initial speciation rate of 0.619 ± 0.075 species Myr^{-1} and a carrying capacity of 22.76 ± 1.12 species. This bound is extremely close to the current number of species in the European clade, which is 22. The North American species undergo their own diversity dynamics and follow a pure birth process with a speciation rate of 0.355 ± 0.071 species Myr^{-1}.

DISCUSSION

Short-lived species may have promoted the geographical expansion of *Androsace*

Our biogeographical reconstruction suggests that Asia is the ancestral region of *Androsace*, as hypothesized earlier (Kress, 1965; Wang *et al.*, 2004). The biogeographical history of the genus is characterized by two intercontinental dispersal events followed by diversification bursts: from Asia to Europe in the early–middle Miocene (nodes A/B; Fig. 1); and from Europe to North America in the late Miocene–Pliocene (nodes C/D, Fig. 1). One striking result is that almost all the ancestors that have expanded from one continent to another were probably short-lived species (nodes A, B, F, G, H; Fig. 1) according to the ancestral reconstruction inferred by Boucher *et al.* (2012). This is congruent with the contemporary observation that the large majority of *Androsace* species with widespread distributions are short-lived [*A. elongata*, *A. erecta* Maxim., *A. filiformis* Retz., *A. lactiflora* Kar. & Kir., *A. maxima* L., *A. septentrionalis* L. and *A. umbellata* (Lour.) Merr.]. The biogeographical expansion of *Androsace* has thus apparently been triggered by the high migration potential of annual species (e.g. Lavergne *et al.*, 2012), which have rapid population growth (due to short generation times) and lighter seed mass (mean seed mass was 1 mg over 38 measured taxa, Table S4 in Appendix S2), and by the preference for open habitats of short-lived *Androsace*, which may provide better conditions for seed dispersal (Nathan *et al.*, 2008).

Surprisingly, the ancestor that colonized North America from Europe was most probably a long-lived species (Boucher *et al.*, 2012). The connection of the *Douglasia* clade, which has an amphi-Beringian distribution (i.e. it is found in the Arctic areas around the Bering Strait), with European ancestors was already suggested by Schneeweiss *et al.* (2004) although they did not explicitly test any particular biogeographical scenarios. Since the ancestor of *Douglasia* would have arrived during the Pliocene, the so-called North Atlantic land bridge was no longer available as a migration route (Tiffney, 1985; Milne & Abbot, 2002; Denk *et al.*, 2010). Two plausible scenarios would be a LDD event over the Atlantic Ocean, or a gradual eastward migration through Asia followed by posterior extinction of Asian populations (Schneeweiss *et al.*, 2004). However, LDD seems a more parsimonious explanation, being in line with the monophyly of the amphi-Beringian species and the increasing evidence for trans-oceanic LDD (de Queiroz, 2005). *Androsace* seeds have no specific dispersal adaptations (Anderberg & Kelso, 1996), but their small size may make them susceptible to rare LDD events by wind. Although our sampling is incomplete (several Asian species are lacking), the available morphological and karyological evidence suggests that species missing from our study would probably not fall within the North American–European clade (Anderberg & Kelso, 1996).

Cushion life form probably fostered speciation in *Androsace*

Previous studies have shown that the cushion life form is a key morphological innovation in *Androsace* (*sensu* Miller, 1949), which enabled the occupancy of alpine niches due to its dense canopy that buffers it from temperature variations (Boucher *et al.*, 2012), but evidence was lacking that this trait also fostered species diversification. Here we have shown that cushions probably spurred diversification in the clades where they emerged, as expected with key innovations (Glor, 2010). This result may seem counterintuitive in terms of the extreme longevity of cushion species (up to several hundred years; e.g. Morris & Doak, 1998) and the type of environment in which these bursts of diversification occurred. Cushion species are associated with extremely cold environments (Boucher *et al.*, 2012) that are among the coldest on Earth (Körner, 2011). This is contrary to the common expectation that short life history alone promotes diversification, and to theoretical studies suggesting that

Table 2 Performance of diversification models based on the Akaike information criterion (AIC) and parameter estimates (λ, speciation rate; μ, extinction rate; *K*, carrying capacity). For each clade of *Androsace*, the model having the lowest mean AIC over the 100 trees is considered the best and other models are compared to it based on their ΔAIC (mean and standard deviation over the 100 trees are reported). Thus the best model has a ΔAIC of zero. Row names indicate the model types: PB, pure birth model; BD, birth–death model; DDL, density-dependent model with no extinction; DDL+E, density-dependent model with extinction. The last four models were only fitted to the North American (NA)–European (E) clade, with decoupling of diversification dynamics within the North American clade from the rest of the clade: DDL/PB, a model where European species undergo a density-dependence without extinction and North American species follow a pure-birth process; DDL+E/BD, the same model with extinction in both clades; DDL/DDL, a model where both European and North American species undergo density-dependence with no extinction, but at different paces and with different carrying-capacities; DDL+E/DDL+E, the same model with extinction.

	Central Asian clade (32 species)				North American–European clade (32 species)			
	ΔAIC	λ	μ	*K*	ΔAIC	λ	μ	*K*
PB	0	0.123 ± 0.004	0	$+\infty$	4.67 ± 0.91	0.238 ± 0.034	0	$+\infty$
BD	1.42 ± 0.27	0.172 ± 0.018	0.081 ± 0.023	$+\infty$	6.67 ± 0.91	0.238 ± 0.034	$8.50 \times 10^{-8} \pm 8.50 \times 10^{-7}$	$+\infty$
DDL	2.00 ± 0.00	0.123 ± 0.004	0	$2.62 \times 10^{6} \pm 2.12 \times 10^{6}$	2.48 ± 0.77	0.550 ± 0.061	0	37.0 ± 1.67
DDL+E	3.51 ± 0.96	2.00 ± 0.439	0.325 ± 0.027	70.14 ± 1.45	4.35 ± 0.95	0.723 ± 0.148	0.070 ± 0.035	35.5 ± 11.9
DDL/PB	—	—	—	—	0	$\lambda_E = 0.624 \pm 0.075$	$\mu_E = 0$	$K_E = 22.7 \pm 1.12$
						$\lambda_{NA} = 0.364 \pm 0.071$	$\mu_{NA} = 0$	$K_{NA} = +\infty$
DDL+E/BD	—	—	—	—	3.86 ± 0.12	$\lambda_E = 0.738 \pm 0.115$	$\mu_E = 0.039 \pm 0.022$	$K_E = 22.0 \pm 1.01$
						$\lambda_{NA} = 0.364 \pm 0.071$	$\mu_{NA} = 1.84 \times 10^{-5} \pm 0.071$	$K_{NA} = +\infty$
DDL/DDL	—	—	—	—	0.81 ± 0.65	$\lambda_E = 0.628 \pm 0.075$	$\mu_E = 0$	$K_E = 22.7 \pm 1.12$
						$\lambda_{NA} = 0.868 \pm 0.228$	$\mu_{NA} = 0$	$K_{NA} = 10.39 \pm 1.55$
DDL+E/DDL+E	—	—	—	—	4.23 ± 0.48	$\lambda_E = 0.743 \pm 0.117$	$\mu_E = 0.041 \pm 0.023$	$K_E = 22.7 \pm 1.12$
						$\lambda_{NA} = 2.00 \pm 0.824$	$\mu_{NA} = 0.230 \pm 0.166$	$K_{NA} = 9.73 \pm 3.13$

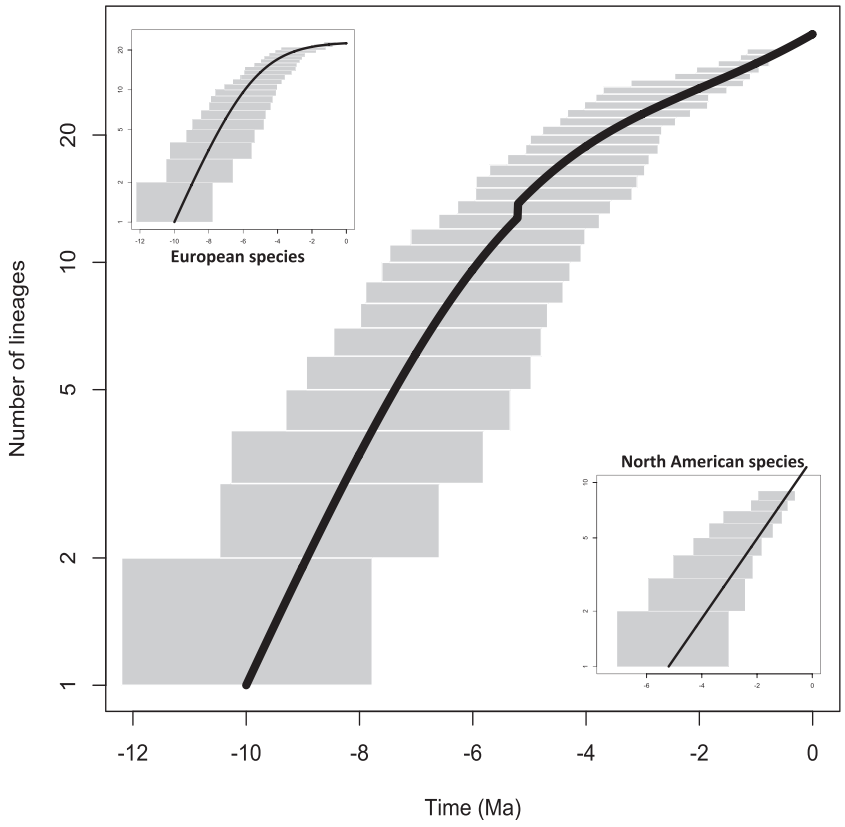

Figure 3 Diversification of the whole North American–European clade (main plot), the European species only (upper left plot), and the North American subclade (lower right plot) of *Androsace*. The grey area represents the upper and lower bounds of all lineage-through-time (LTT) plots obtained on the 100 trees. The black line shows the clade richness predicted by the most likely model with parameters estimated on the consensus tree.

warmer environments favour speciation due to higher metabolic rates (Allen *et al.*, 2006). However, it can be explained by the ecological opportunity (Simpson, 1953; Glor, 2010) that high alpine environments represented for *Androsace* ancestors. This opportunity was probably provided by: (1) active orogenic areas providing new physical environments; (2) progressive climate cooling (Zachos *et al.*, 2008), resulting in the emergence of the alpine biome; and (3) the emergence of the cushion life-form, providing a morphological innovation that allowed new niches to be explored.

Androsace provides a case where the effects of ecological and biogeographical processes that promote diversification overcome any limits on diversification rates that arise from environmental stress. This example is, however, not the first of its kind. Several large radiations of pachycaulous plants in the alpine tropics have already been documented (Monasterio & Sarmiento, 1991; Knox & Palmer, 1995), some of them with exceptionally high speciation rates (more than 2 species Myr^{-1} on average in *Lupinus*; Hughes & Eastwood, 2006). All these alpine radiations support Schluter's (2000) hypothesis that ecological opportunity not only increases the probability of ecological speciation, but can also spur diversification by increasing the opportunities for reproductive isolation. Indeed, by opening the way to alpine environments, cushion and pachycaulous life forms provided access to highly fragmented habitats (i.e. mountain tops), thereby increasing the chances of allopatric speciation.

Replicated radiations in distinct mountain ranges and evidence for geographical limitations on diversity

Focal analyses of the three radiations that occurred in Asia, Europe and North America lead to two diversification patterns. The radiation of Asian species shows evidence of constant speciation through time, which could indicate that this clade is still far from having reached any upper diversity limit in Central Asia. However, the fact that all diversification models had similar AIC scores indicates that the low sampling of our phylogenies for this clade probably reduces the statistical power of our analyses and prevents solid inferences on the tempo of speciation. At the same time, the radiation of the better-sampled clade of European species showed evidence for density-dependent speciation, a pattern consistent with other studies (e.g. Phillimore & Price, 2008; Rabosky & Lovette, 2008; Etienne *et al.*, 2012). European *Androsace* are apparently close to their estimated carrying capacity and current speciation rates are very low, but the estimated speciation rate at the beginning of the radiation in Europe was relatively high for a group of plants in a temperate continental settings (Klak *et al.*, 2004; Hughes & Eastwood, 2006). Conversely, the clade of North American species made up of all *Douglasia* plus *A. triflora* shows no signs of a slowdown in diversification.

Relatively high speciation rates at the beginning of the European and North American radiations may be explained

by the fragmented landscape of the areas where *Androsace* is found. They may also be due to past climatic oscillations (Zachos *et al.*, 2008), which have alternately connected and disconnected regions of suitable climate for *Androsace* species – a phenomenon known to promote speciation (Kadereit *et al.*, 2004; Aguilée *et al.*, 2011). The North American radiation could also have been promoted by Pliocene–Pleistocene climatic cooling: the beginning of the *Douglasia* diversification coincides with the onset of the Arctic ecosystem, *c.* 3 Ma (Matthews & Ovenden, 1990; Murray, 1995). It is interesting to note that, within the Arctic flora, the radiation of *Douglasia* is an exception, as most Arctic plant species have been shown to originate from non-arctic lineages (Hoffmann & Roser, 2009).

In the European clade, this initial phase of rapid radiation has been followed by a slowdown caused by density dependence. Such diversity bounds are usually thought to arise when ecological space is divided between coexisting species originating from the same radiation, progressively filling out the entire niche space (Rabosky, 2009). In the case of *Androsace*, this explanation is unlikely, because cushion species exhibit few ecological differences (either in their resource use, morphology or in their biotic interactions) and low levels of sympatry. Additional analyses of climatic vicariance indeed show that, besides the differences between life forms, partitioning of the climatic space has not played a major role in the diversification of *Androsace* (Appendix S2). Thus, the radiation of *Androsace* has apparently been little driven by adaptation to different ecological niches, and it should be considered more as an example of non-adaptive radiation (Gittenberger, 1991).

The observed density-dependence in European *Androsace* may probably be attributed to a progressive filling of the geographical space by species with similar ecological niches (Schluter, 2000; Rundell & Price, 2009), as previously documented in several non-adaptive radiations of alpine plants (Kadereit *et al.*, 2004). The fact that current species richness in European *Androsace* almost reaches the estimated carrying capacity of this clade suggests that geographical filling might be complete in Europe. This agrees with the observation that *Androsace* species occur in all alpine mountain ranges of Southern Europe and that most European species have small ranges, thereby reducing the chances for allopatric speciation. On the other hand, given the much larger area available for *Douglasia* species in Alaska and the Rocky Mountains, it is logical that this young clade does not yet show strong signs of density-dependent regulation, and it is probably still in a phase of active diversification.

The fact that models with no extinction were favoured in all cases should not be interpreted as evidence for null extinction in *Androsace*. We cannot totally exclude the hypothesis that cushion species experienced reduced extinction rates (for instance, their extreme longevity could help to survive rapid environmental fluctuations) instead of having higher speciation rates. The difficulty of estimating extinction rates from phylogenies of extant taxa alone is a major area of concern in macroevolution (e.g. Purvis, 2008; Rabosky, 2010). Information from the fossil record could be useful for this purpose, but it is non-existent for *Androsace* and very scarce for Primulaceae. Alternatively, one could separately examine different extant clades in order to detect positive extinction rates in some clades that would have otherwise been masked by recently radiating lineages (e.g. Morlon *et al.*, 2011). We did account for rate heterogeneity in *Androsace* in that we studied three clades separately, while allowing diversification rates to vary across life forms, but still failed to detect non-null extinction rates. Since it is possible that these subdivisions may still have blurred the signal of extinction in other clades, it was not possible to distinguish speciation rates from net diversification rates.

CONCLUSIONS

Androsace has several characteristics that could have doomed the genus to remain geographically restricted and species-poor. Most *Androsace* species have low dispersal abilities and occupy very harsh and disconnected habitats. However, in spite of these obvious limits to diversification, *Androsace* has expanded throughout the Northern Hemisphere and has experienced some periods of rapid diversification. Interestingly, two types of life form have played complementary roles in this success story. First, short-lived ancestors allowed range expansion throughout Eurasia thanks to their better dispersal abilities and their temperate climatic tolerance. Second, cushion species appeared independently at least twice and promoted diversification in the Himalayas, Europe and North America by enabling the colonization of high alpine niches, which in turn lead to allopatric speciation in fragmented alpine habitats. Although convergent evolution towards the same key innovation (i.e. cushion life form) in Europe and Asia reveals strong ecological and evolutionary determinism, important differences remain in the timing, tempo and rate of species radiations in Asia, Europe and North America. Perhaps the most striking contingency is the LDD event that occurred from Western Europe to North America, probably across the North Atlantic, and provoked the recent radiation of *Douglasia* species. The history of *Androsace* thus illustrates how deterministic and contingent events can contribute to a clade's evolutionary success and advances our understanding of the origins of diversity in arctic and alpine ecosystems. Further research is needed to confirm the role of dispersal, habitat fragmentation and life form evolution on the diversification and distribution of alpine plants. This should enable us to understand why alpine ecosystems are relatively rich in spite of their harsh environmental conditions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary methods.
Appendix S2 Supplementary results.

BIOSKETCH

The authors of this article work in a research group called EMABIO (Evolution, Modelling and Analysis of Biodiversity), which is hosted by the French CNRS and the University of Grenoble. The authors are involved in the TEEMBIO ERC project. One of the main axes of this multidisciplinary project is to improve the understanding of how evolution shapes species ranges at micro- and macro-evolutionary scales.

Author contributions: All authors contributed to the design of the study; C.R. and F.C.B. ran the analyses and led the writing, with substantial contributions from W.T. and S.L.

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CHAPITRE 4.

HISTOIRE EVOLUTIVE ET BIOGEOGRAPHIQUE DE LA FORME DE VIE EN COUSSIN CHEZ LES ANGIOSPERMES

Introduction

Nous avons vu comment l'apparition de la forme de vie en coussin a permis à certains membres du genre *Androsace* d'occuper les environnements alpins et a contribué au succès évolutif de ce genre en stimulant sa diversification. Or, la forme de vie en coussin n'est pas apparue uniquement dans le genre *Androsace*, mais est aussi portée par des centaines d'espèces de plantes dans le monde.

Dans ce dernier chapitre je me suis intéressé à l'histoire de la forme de vie en coussins chez les Angiospermes, afin (i) de mesurer l'envergure de cette convergence évolutive mais aussi (ii) de comprendre les facteurs environnementaux, historiques et géographiques qui ont permis son apparition. Pour cela, il a d'abord été nécessaire de recenser toutes les espèces en coussin du monde et d'en réaliser une typologie. Ce travail long et fastidieux a été principalement réalisé par Serge Aubert et ses résultats sont présentés dans l'article 4.1. Ensuite, en combinant cette base de données et la phylogénie des familles d'Angiospermes, nous avons pu étudier l'histoire de la forme de vie en coussins chez les Angiospermes dans l'article 4.2.

En changeant d'échelle par rapport aux autres chapitres de ma thèse, j'ai dû composer avec le manque de précision des données sur un groupe aussi large que les Angiospermes et adapter la méthodologie en conséquence. Les résultats présentés dans ce chapitre sont donc très généraux et demandent à être complétés par d'autres études plus fines. Ils font cependant écho aux résultats trouvés sur le genre *Androsace* et fournissent des éléments clefs pour la compréhension de l'histoire et de la diversité actuelle des flores des régions alpines et arctiques du globe.

Tout d'abord, notre recensement a mis en évidence que le nombre d'espèces en coussin est beaucoup plus élevé que celui qui avait été donné il y a un siècle par Hauri & Schröter (1914) et qui a été repris par tous les auteurs depuis (par exemple Reid et al. 2010). Notre base de données contient en effet 1311 espèces de plantes en coussin (en incluant également les espèces formant des tapis), alors qu'Hauri & Schröter (1914) en recensaient 200. La forme de vie en coussin est donc une convergence évolutive très répandue chez les Angiospermes et nous avons montré que les coussins compacts sont apparus au moins une quarantaine de

fois de manière indépendante au sein des Angiospermes (ce chiffre étant probablement très largement sous-estimé, voir article 4.2).

Nous avons ensuite établi que les coussins appartiennent à des familles qui occupent des climats significativement plus froids (et dans une moindre mesure plus secs) que la moyenne des familles d'Angiospermes. Ce résultat confirme que la forme de vie en coussin, dont nous avons montré qu'elle est une innovation clef chez *Androsace* (article 3.1), semble être une adaptation aux climats alpins et arctiques dans l'ensemble des Angiospermes. De manière intéressante, les familles contenant des coussins ne sont pas réparties de manière aléatoire au sein des Angiospermes, mais sont plutôt regroupées. Ceci suggère que certains traits pourraient être prérequis pour que la forme de vie en coussin puisse apparaître.

Enfin, nous avons identifié des régions où le nombre d'espèces en coussin est particulièrement important par rapport à leur surface, qui sont l'Himalaya, les Andes, la Patagonie et l'île Sud de la Nouvelle Zélande. Nous avons montré que ces régions ont probablement joué des rôles différents dans la diversité actuelle des coussins. Ainsi, alors que l'Himalaya, les Andes et la Nouvelle Zélande ont plutôt été des berceaux de diversification pour les coussins, la Patagonie a également joué un rôle de plaque tournante en permettant à des espèces de coussins de transiter entre l'Amérique du Sud et les régions australes.

ARTICLE 4.1

UN CATALOGUE GLOBAL DES PLANTES EN COUSSIN, 100 ANS APRES HAURI ET SCHROTER

A worldwide catalogue of cushion plants 100 years after Hauri and Schröter

Serge Aubert, Florian C. Boucher, Sébastien Lavergne & Philippe Choler

Key words: alpine plants, Angiosperms, biogeography, evolutionary convergence, life form

Abstract

Cushion plants have long fascinated botanists for their ability to cope with extreme environments in most mountains and arctic regions of the world. One century ago, a first worldwide catalogue of species forming cushion life-form was published by Hauri & Schröter (1914). Here, we defined a simplified typology of cushion plants and developed an updated catalogue based on available information in floras and catalogues but also in efloras and virtual encyclopedias, which were screened by the means of automated data-base queries. We thus established a list of 1311 cushion-forming species distributed in 272 genera and 63 families of angiosperms. Compact cushions represented 678 species, among which 587 species with a hemispherical shape, 91 species with flat to mat shape. 398 species corresponded to non-compact hemispherical cushions, and 270 species were thorny. The list of cushion species has significantly increased since Hauri & Shröter, due to new species discovery, important works of species listing and inventories, and the improved procedures of data-base screening implemented here. Uncertainties in the delineation of the cushion life form are discussed, notably for non-compact growth forms. A website has been launched to display the catalogue and permit a collaborative improvement of the database. The distribution of the species is presented on the basis of the World Geographical Scheme for Recording Plant Distributions and Global Biodiversity Information Facility (GBIF) data. This catalogue will serve as a reference database for further analyses on the biogeography and evolutionary history of cushion plants.

Introduction

Amongst the extraordinary diversity of life forms displayed by angiosperms, cushion-forming species have long fascinated botanists and alpine plant *aficionados*. Cushion plants are known as *plantae pulvinatae* in Latin*, plantes en coussin* (or *coussinet*) in French*, plantas en cojín* or *almohadilla* in Spanish and *piante a cuscinetto* in Italian. They were first associated to the high altitude and cold ecosystems of the Alps (Raunkiaer 1934) and their remarkable habit then puzzled the botanists who travelled to newly investigated mountainous areas, notably the Andes, Patagonia and Tierra del Fuego (Weddel 1855, Reiche 1893, Skottsberg 1909, Weberbauer 1931) or the mountains of South New Zealand (Cockayne 1912). These areas host a very high diversity of cushion plants in families absent from Holarctic regions or in families showing no examples of cushion habit in Holarctic regions, e.g. the genera *Azorella* (Apiaceae in the Andes and Subantarctic islands), *Petunia, Benthamiella* (Solanaceae from Patagonia), *Raoulia, Haastia* (Asteraceae from New Zealand. It was thus early noted that cushion plants may dominate subalpine and alpine ecosystems way beyond the European alpine region. In addition, the expeditions in the Irano-Turanian floristic region allowed the measure of the importance of thorny woody cushions, which are typical of high degree of climatic continentality and long summer drought (von Heldreich, Boissier 1867-1888).

Many studies have focused on the moss campion *Silene acaulis*, a widespread arctic alpine species, as a model species to understand the ecophysiology of cushion plants (e.g. Körner 2003, Molenda et al 2012). The cushion form represents an efficient trap for heat and water, with a maximum reduction of losses due to the spherical shape (lowest surface-to-volume ratio). The cushion habit, present in hundreds of plants belonging to various families and genera, represents a good example of evolutionary convergence across phylogenetically unrelated taxa in various cold and/or dry regions of the world (Körner, 2003; Sklenář, 2009). Cushion plants have a key role in the communities, acting as nurse species, with significantly more plant (and arthropods) species growing within cushions than outside their canopy (for review, Reid et al 2010). Alpine cushion plants have also been recently shown to inhibit the loss of phylogenetic diversity in severe environments: these keystone species act as micro-refugia by facilitating less stress-tolerant lineages (Butterfield et al 2013), and are also associated with particular communities of bacteria and fungi (Roy et al. 2013). Combined with the extraordinary individual longevity of adult plants (Morris & Doak D 1998; Halloy 2002), cushion species may thus be important ecosystem engineers, participating in the long-term stability of high alpine biotic communities, probably the most severe climate on earth (Körner 2011).

The first review on cushion plants was made by the German botanist Karl Reiche (1893), the author of the first flora of Chile. Hans Hauri and Ludwig Schröter (1914) proposed a first typology and a catalogue of 338 cushion species including 200 species of compact radial cushions termed « Radialvollkugelpolster » in German to express several of their morphological features: radial-growing (“radial”), solid peat-accumulating (“voll”), hemispherical (“kugel”) and cushions forming (“polster”). The authors pointed out the diversity of families (34) and genera (78) in which cushion species were found and discussed their geographical distribution. These original numbers have been echoed in different later reports (eg Ruffier-Lanche 1964, Arredondo-Núñez et al. 2009 ; Reid & al 2010). Then, a major contribution was made by Werner Rauh (1939), a student of the famous plant morphologist Wilhem Troll. Rauh dedicated his phD to the plants with cushion growth form, with a typology including a fine description of the growth and organization (Figure 1),

and outstanding drawings of representative species among the 350 species he described (including many new species added to Hauri and Schröter’s work).

The description of emblematic compact cushion species such as *Androsace helvetica* (Primulaceae of the Alps), *Azorella compacta* (Apiaceae of the central Andes) or *Raoulia eximia* (Asteraceae of New Zealand mountains) suggests that the definition of cushion plants should be rather easy.

However, distinguishing cushions from mat forming plants has often been difficult (Raunkiaer 1934, Rauh 1939, Gibson & Hope 1986, Parsons & Gibson 2009). Parsons & Gibson (2009) defined cushion plants as chamaephytes or hemicryptophytes growing singly and taking on a hemispherical (“kugel” in German) or subhemispherical to

low ("flach" in German) shape, due to the close branching of their shoots and their short internodes. The leaves are usually small, which allows the shoots to be very closely compacted and the margins of the shoot canopy normally extend downwards to reach ground level. Cushion plants form a continuum from hard, compact species that accumulate peat within their shoots ("voll") to soft, loose, non-peat-accumulating species ("hohl"). Examples of intergradation between the various types defined below are common and some species only occasionally take on a cushion form (Rauh 1939). For example, *Azorella selago* may appear as a dense cushion or as a dense mat (Moore 1983), and the Asteraceae *Alchemilla subnivalis, Helichrysum newii* and *H. gofense* shift from an erect shrub habit to a prostrated cushion habit along an altitudinal gradient on the high afro-alpine mountains (Hedberg 1986). Some plants may also appear as solitary rosettes or as cushions, ie *Phyllactis rigida* in the Andes or *Potentilla foersteriana*, *P. brassii* in tropical alpine New Guinea (Mangen 1993, Jorgensen & Ulloa Ulloa 1994).

One century after the landmark study of Hauri and Schröter (1914), we decided to update the catalogue in terms of number of species, agreement to APGIII nomenclature, and geographical information. To do so, we defined a simplified typology of cushion plants and developed an updated catalogue based on available information in floras, and catalogues but also in efloras and virtual encyclopedias, which were screened by the means of semi-automated data-base queries. A website has been launched to display the catalogue and permit a collaborative improvement of the data-base.

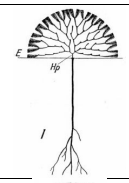
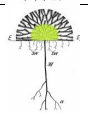
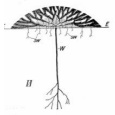
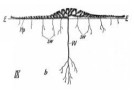
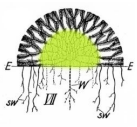
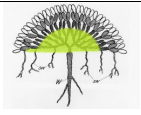
Major types of cushions	Subtypes	Examples	Drawings	Images
"Radialkugelpolster" Radial hemisphaerical cushions	**"Polsterbäume"** Radial cushion trees	*Dracaena draco*		
	"Kugelsträucher" Radial cushion shrubs	*Bupleurum fruticosum*		
	"Hohlkugelpolster" Radial hollow hemispherical cushion **HKP**	*Oxytropis cornuta* (Fabaceae)		
	"Vollkugelpolster" Radial solid hemispherical cushion **VKP**	*Androsace helvetica* (Primulaceae)		
"Radialflachpolster" Radial low cushions	**"Hohlflachpolster"** Radial hollow low cushion **HFP**	*Azorella trifurcata* (Apiaceae)		
	"Vollflachpoolster" Radial solid low cushion **VFP**	*Silene acaulis* (Caryophyllaceae)		
"Kriechpolster" Creeping cushions	**KP**	*Saxifraga oppositifolia* (Saxifragaceae)		
"Rasenpolster" turf cushion	**"Kugelrasen"/ "Flachrasen"** Hemispherical/Low turf cushion **RaP**	*Patosia clandestina* (Juncaceae)		
"Rosettenpolster" Rosette cushions	**"Kugelpolster"/ "Flachpolster"** Hemispherical/Low rosette cushion **RoP**	*Phyllactis rigida* (Valerianaceae)		
"Sukkulentepolster" Succulent cushions	**SP**	*Austrocylindropuntia floccose* (Cactaceae)		
"Polstermoose" cushion mosses		*Leucobryum spp.*		

Figure 1. Typology of cushion plants of Rauh (1939) with corresponding representative drawings and images.

Material and methods

The typology of cushions

Although sharing major morphological features, cushion plants vary in their vegetative and root architecture. Rauh (1939) improved the terminology proposed by Hauri and Schröter (1914) and proposed the most extensive typology of cushion plants which he used to classify ca. 350 species. As many other authors did we excluded the "cushion trees". However, other species were not always easy to assess to a given Rauh's type of cushion since descriptions from various authors are not all made with the same criteria. We therefore decided to simplify Rauh's typology and document several parameters given in Table 2. The two major criteria that we used in our typology are the form of the cushion and its degree of compactness, two parameters usually given by most of the descriptions. Table 2 summarizes all characteristics considered to elaborate this typology.

As different individuals of the same species may vary from one type of cushion to another, we also recorded variability (0 referring to the absence of variability to 2 when the species may appear as solitary or as cushion). Finally, additional parameters like woodiness, succulentness, thorniness, root system (poorly documented in most of the floras) and the length of the flower or inflorescence peduncle were recorded whenever possible.

When the description of the species included two habits (e.g. mat and cushion), the list refers to a dual habit (e.g. "mat or hemispherical cushion-forming plant" for *Veronica caespitosa* is coded as "C_M"). Similarly, for species growing either as cushion or solitary, the dual code "C_0" was used, "0" referring to the solitary habit (absence of cushion).

Elaboration of a cushion species checklist

We decided to include only Angiosperm species in our list and to exclude 'cushion trees' (Rauh 1939). Species were listed as cushions if they were explicitly described as 'cushion', 'pulvinate' 'hummock-forming' or 'mounds' or variants (e.g. "tufted to cushion-forming" for *Minuartia juniperina* in Davis 1967) and combinations of these terms (e.g. "perennial, densely cespitose, cushion-forming" for *Paronychia pulvinata* in eFlora of North America). When possible, species described as 'densely tufted' or 'densely caespitose' were analyzed from different sources of literature in order to evaluate if their compactness was sufficient to be considered as cushion-forming species (e.g. "densely cespitose to pulvinate" for *Draba oligosperma* in eFlora of North America). Finally, species described as 'mats' were only considered as cushion species when mats are characterized as compact or when transitions to hummock or low cushions are described, e.g. "compact mat to hummock-forming subshrub" for the Australian Goodeniaceae *Lechenaultia pulvinaris* (encyclopaedia.alpinegardensociety.ne), "densely mat to cushion-forming" for *Minuartia rimarum* (Davis 1967), or "mat to low cushion-forming" for *Werneria aretioides* (encyclopaedia.alpinegardensociety.net). Nevertheless, the difference between mat-forming and low cushion-forming species is not easy to delimitate (Foweraker 1917) and would require a detailed analysis of the architecture of the corresponding samples.

The bases for the establishment of the catalogue were the lists of Hauri and Schröter (1914) and Rauh (1939). In order to be as exhaustive as possible in our listing of cushion species, various sources of information were used including floras, efloras, catalogues, monographies, virtual encyclopedias, and virtual herbaria (listed in Table 1). We used reviews and monographies on certain types of cushions such as cushion bogs (Godley 1978) and on genera comprising cushion species, notably for *Acaena* (Marticorena 2006), *Dionysia* (Lidén 2007), *Abrotanella* (Swenson 1995), *Brayopsis* and *Eudema* (Al-Shehbaz 1990), *Baimashania* (Al-Shehbaz 2000), *Kelleria* and *Drapetes* (Heads 1990), *Azorella, Laretia*, and *Mulinum* (Nicolas & Plunkett 2012), *Junellia* (O'Leary & al 2011), *Opuntia* (Ritz et al 2012). The online Plant Encyclopedia of the alpine garden society (http://encyclopaedia.alpinegardensociety.net/) and the Rock Garden Plants Database (http://www.kadel.cz/flora/) were helpful resources, particularly for species growing in regions with no available flora. We also used the IUCN Red List of Threatened Species (http://www.iucnredlist.org/). Finally, we used internet requests to search in the following efloras (http://www.efloras.org/, 2013): North America, China, Pakistan, Chile, and the annotated checklist of the flowering plants of Nepal. A script of automated request

(supplementary material) on efloras was developed with key words including “pulvin” (cf pulvinate, pulvinatus/a, pulvinaris, pulvinatum/a, pulviniformis), “densely tufted”, “densely caespitose”,“cushion”, “hummock”, “bolster”, “aretioides” (referring to the former name of a section with hard cushions in the genus *Androsace*), “musciformis, muscoides, muscosa, or bryoides” (reference to cushion-moss habit), "azorella, azorelloides, or azorellacea”, “oreoboloides”, “saxifragoides”, and "pycnophylloides” (reference to the cushions in the genera *Azorella, Oreobolus, Saxifraga, and Pycnophyllum, respectively).*

We chose to adopt the nomenclature of *The Plant List* (http://www.theplantlist.org/), the online list of vascular plants developed by the Royal Botanic Gardens, Kew and Missouri Botanical Garden, in collaboration with various contributors. The nomenclature of *The Plant List* was not followed for some genera not updated in this list, e.g. *Convolvulus*. Synonymies were verified and family names updated to APGIII (Stevens 2001).

The geographical data

The distribution of each species has been listed according to the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001). This scheme defines four scales, from continents (level 1 with 9 polygons and level 2 with 52 polygons) down to country or province levels (level 3 with 369 polygons and level 4 with 610 polygons). Using all sources of information listed above, we managed to document at least the level 3 distribution for all species. The level 4 distribution was documented for 85% of the species.

The Global Biodiversity Information Facility (GBIF) established in 2001 to encourage free and open access to biodiversity data, via the Internet, was also used. We implemented a R code for the automated retrieval and analysis of GBIF records. GBIF data was found especially useful to add new level 4-polygons. We checked manually all GBIF entries to remove outliers. For ca. 250 species on 1300 species, GBIF permitted to increase the distribution of species with neighboring level 4-polygons, as compared to the floras. By example, according to the *Catalogo de las Plantas Vasculares del Cono Sur* (Zuloaga et al 2008), *Azorella madreporica* grows in Chile (regions III, IV, V, VI, VII) and Argentina (regions Chubut, Mendoza, Neuquen, Río Negro, Santa Cruz, and San Juan). GBIF data permitted to add two neighbor regions of Chile (i.e. region IX and Metropolitan region). Conversely, some mistakes in GBIF data were pointed out and discarded. For instance, *Acantholimon acerosum* mainly appeared in Turkey, Armenia, Iraq, Afghanistan and Greece but also with a spot in Canada corresponding to an herbarium specimen (collected in Turkey) of the University of British Columbia Herbarium (UBC). Despite the use of all these sources of information, we acknowledge that the geographical distribution of many cushion plants remains poorly documented. This is particularly true in regions that have been less intensively surveyed by botanists (e.g. Central Asia) or that are less precisely described by the geographic scheme we used (e.g. Siberia). This is meant to be improved through the development of a participative project, which will be possible by a website allowing to browse the present database and submit additional information.

Results and discussion

The primary aim of this work is not to provide a quantitative analysis of cushion species biogeography and macroevolution, but rather to detail the elaboration of a checklist of species with a cushion growth form, which will serve as a basis for future studies about the climatic adaptations and the evolutionary origins of such species. Our revised catalogue is available at the following address: www.cushionplants.org and summarized in Table 3. It contains a list of 1311 species belonging to 273 genera and 62 angiosperm families, including both monocots and eudicots. Compact cushions represented 678 species, among which 587 species with an hemispherical shape and 91 species with a flat shape. 398 species corresponded to non-compact hemispherical cushions and 270 thorny species were recorded. These numbers far exceed the results reported one century ago by Hauri & Schröter (1914): 200 species of compact hemispherical cushions and 138 other cushions, belonging to 34 families and 78 genera. Families having the highest number of cushion species are Caryophyllaceae (165 sp.), Fabaceae (146 sp.), Asteraceae (126 sp.) and Saxifragaceae (123 sp.) (Table 3).

Many reasons may explain the discrepancy between our checklist and the one of Hauri & Schröter (1914). First, many new species have been described, and many species checklists, inventories or catalogues have been published over the last century and we multiplied the ways to take them into account using available floras, efloras, catalogues, and virtual encyclopedias. Second, we may have used a more inclusive definition of cushions. It is clear that, except for the compact (hard) hemispherical cushions, botanists may have diverging ways to consider and classify plant life forms. Therefore, the status of cushion plants usually differs from one flora to the other, according to the various botanists who described them. This is particularly true for non-compact densely tufted cushions with intermediate cases between loosely tufted/tufted/densely tufted/densely tufted cushion-forming. For example, the genus *Leontopodium* is absent in in Hauri & Schröter 1914. In Himalayas, according to eflora of China, this genus has one species among compact hemispherical cushions (*L. haastioides*), one among compact low cushions (*L. pusillum*, present in Rauh 1939), and two species described as "perennial pulvinate herbs" (*L. aurantiacum* & *L. delavayanum*). These species were integrated as cushion species (eflora of China). The same holds true with various species of *Townsendia* described as "perennials ± pulvinate" in the eflora of North America (eg *T. hookeri*), as perennial rosettes in the online Plant Encyclopaedia of the alpine garden society (http://encyclopaedia.alpinegardensociety.net)and as a cushions in the Rock Garden Plants Database (http://www.kadel.cz/flora/).Two species among ca. 10 related species *, T. gypsophila and T. hookeri*, were inserted in our catalogue as non-compact tufted cushions.

Similarly, the genus *Asperula* contains various species of non-compact cushions in Greece and Turkey. Ten species were inserted in our catalogue as hemispherical, flat or tuftet cushions while none was in Hauri & Schröter (1914) or Rauh (1939). Various other species described as densely caespitose with a tendency to form cushions were excluded from our list. As a result of these differences, the number of non-compact cushions, notably tufted cushions, may therefore be higher in our catalogue. Another source of uncertainties comes from the two thorny non-compact cushion-forming genera *Astragalus* and *Acantholimon* : the number of species is very high and the status of cushion is not always clear.

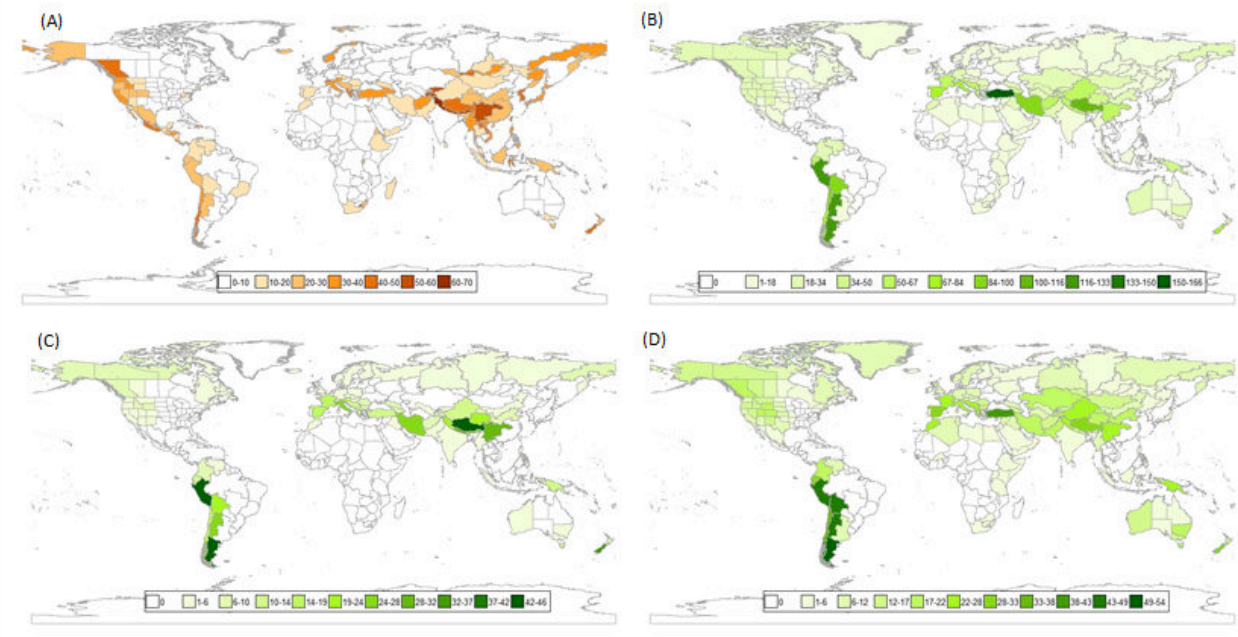


Figure 2. World distribution of cushion plants on the basis of the level 3 of the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001). (A). Area of rugged terrain (%); (B). Number of cushion species (all life forms); (C). Number of cushion species (compact forms only); (D). Number of cushion genera (all life forms).

included in our catalogue. Conversely, various species varying from "tufted" to "densely tufted" which have not been

The status of some species should be discussed, e.g. the hummock grasses (*Triodia* and *Plechtrachne*), such as pincushion spinifex (*Triodia molesta)* which have not been included, although they might be considered as densely tufted cushions. Similarly, some species listed by Parsons & Gibson (2009) in Western Australia were not listed in our catalogue, on the basis of our criteria. A further limitation is due to the species that may form cushions or not. They are documented in the catalogue with the variability parameter not equal to 0. Examples are given with the Valerianaceae *Phyllactis rigida* (Northern Andes) and with *Potentilla foersteriana* (tropical alpine vegetation in New Guinea), both appearing solitary or as a rosette hemispherical cushion.

This catalogue does not intend to be an absolute reference. Particularly for non-compact species, it reflects the subjectivity of the authors who treated all species the same way on the basis of different reports from various floras and botanists. Ideally, a direct analysis of specimen from all species would be necessary, which was not possible in this study. We decided to use an inclusive definition of cushion-forming plants, which may be restricted on the basis on the degree of compactness and on the shape (hemispherical vs. flat and mat). The online catalogue is considered as an evolving and participative database, which will be modified according to argued contributions (suppression of species, inclusion of new species, modification of the status, images, etc.).

The 1311 species of cushion plants are widely distributed in all continents (Figure 2, Table 4). However, some regions show higher densities, notably the mountainous areas. Among them, the richest areas were the Andes and the mountain ranges stretching from the Pyrenees to the Himalayas, notably the Alps, the Anatolian and the dry Irano-Turanian mountains. The cold steppes of Patagonia and Eastern Tierra del Fuego also possess a very high diversity with 114 species in the Argentine regions Chubut, Neuquén, Rio Negro, Santa Cruz and Argentine Tierra del Fuego. At the genera level (Figure 2D), the Andes and Patagonia appear as the richest zones. The Southern Alps of New Zealand also appear as an area of high diversity of cushion plants (74 species). Fewer species were observed in the Rocky Mountains in North America, in the Arctic and in the Siberian regions, and in the dry mountains of Atlas in North Africa and Spain. This tendency had been reported by Hauri and Schröter (1914) who listed 170 species in South America (50% of their total), 54 in Asia (16%), 46 in New Zealand, Kerguelen and Australia (14%), 40 in Europe (12%), 10 in Africa (3%), 9 in Arctic and 8 in North America (Table 4). Interestingly, tropical alpine areas showed major differences, with 39 species in New Guinea, 47 species in Ecuador and only 5 species in Eastern Africa (one of them also present in Western Africa at mount Cameroun).

This catalogue aims to participate to the exploration and explanation of the great biological richness of the mountains of the world carried out by the Global Mountain Biodiversity Assessment (GMBA). It is a first step towards a better understanding of the evolutionary history of the cushion life form and of its anatomic, climatic and biogeographic drivers.

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Continent	Floras, efloras and catalogues
South America	*Catalogo de las Plantas Vasculares del Cono Sur* (Zuloaga et al 2008), *Flora patagonica* (Correa 1967-99), *Flora of Tierra del Fuego* (Moore 1953), *Flora de Chile* (Reiche 1896-1911), eflora of Chile (2013), *Catalogue of the vascular plants of Ecuador* (Jørgensen & León-Yánez 1999), *Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature* (Lutey 1999), the *catalogue of the Flowering Plants and Gymnosperms of Peru* (Brako & Zarucchi 1993), *Flora of Peru* (MacBride 1893), *catalogue of the flowering plants of the Venezuelan páramos* (Briceño & Morillo 2002, 2006).
North America	Eflora of North America (2013), USDA Natural Resources Conservation Service (http://plants.usda.gov/java/)
Africa	Hedberg (1964), the *Flore de l'Afrique du Nord* (Maire 1952-1977), *Flore pratique du Maroc* (Fennane et al 1999, 2007).
Europe	*Flora europaea* (Tutin et al. 1964), *Flora alpina* (Aeschimann et al 2004), *The mountain flora of Greece* (Srid 1986-1991), the *Flora of Turkey and the East Aegean Islands* (Davis 1965-1985), *The thorny-cushions vegetation in Mediterranean Italy* (Nimis 1981).
Asia: Russia, former soviet republics, China, Pakistan, Mongolia, Irano-Touranian areas	*Flora of the USSR* (Komarov & al. 1934-64), *Key to the vascular plants of Mongolia* (Grubov 2001), efloras of North America, China, Pakistan (2013), annotated checklist of the flowering plants of Nepal (2013), *Flora Iranica* (Rechinger 1963), notably vols. 174-179 (genus *Astragalus*), 108 (Plumbaginaceae)
Australasia	*The alpine flora of New Guinea* (Van Royen 1982), Gibson & Hope (1986), Gibson & Kirkpatrick (1985), *Flora of New Zealand* (Allan 1961, Moore & Edgar 1976, Healy & Edgar 1980), *The student's flora of Tasmania* (Curtis 1963-67; Curtis & Morris 1975-1994), *Flora of New South Wales* (Harden 1992-2000; eflora at http://plantnet.rbgsyd.nsw.gov.au), Parsons & Gibson (2009), *The NZ Plant Conservation Network* (http://www.nzpcn.org.nz/)

Table 1. Main sources of floristic information used to document the catalogue.

Key	Code		Description
1	C	Form of cushions	Hemispherical (dome shaped) cushion
	F		Low cushion
	TC		Tufted cushion, densely caespitose
	M		Mat, creeping cushion
	CL		Loose cushion
2	1	Compactness	Compact, hard (peat-accumulating)
	0		Hollow,
	0_1		Intermediate
R	Table 1	Rauh's types	Table 1
3	0/1/2	variability	No/yes/absence or presence of cushion habit
4	0/1/2	woodiness	herbaceous / Woody at base / Woody dwarf shrub
5	0/1	succulentness	No/yes
6	0/1	thorniness	No/Yes
7	P/A/R	Root system	Single pivotal root/numerous adventitious roots/rhizomes
8	0/1/2	Flowers	Flowers sessile/short peduncle/long peduncle

Table 2. Typology of cushions used in the catalogue.

FAMILY	HEMISPHERICAL CUSHIONS		FLAT CUSHIONS		OTHER	GENERA WITH CUCHIONS OR MATS
	COMPACT	NON COMPACT	COMPACT	NON COMPACT		
Acanthaceae	0	1	0	0	0	*Lepidagathis*
Aizoaceae	0	0	0	2	0	*Aloinopsis, Delosperma*
Amaranthaceae	4	3	1	3	0	*Anabasis, Arthrophytum, Hemichroa, Krascheninnikovia, Nanophyton, Ptilotus, Roycea, Sarcocornia*
Apiaceae	24	9	3	3	8	*Aegokeras, Aciphylla, Azorella, Bolax, Bupleurum, Chaerophyllum, Laretia, Mulinum, Trachymene*
Asparagaceae	0	0	0	0	1	*Lomandra*
Asteliaceae	3	0	0	0	0	*Astelia*
Asteraceae	47	25	16	19	19	*Abrotanella, Anaphalis, Anthemis, Argyrotegium, Artemisia, Atractylis, Baccharis, Belloa, Brachyclados, Bryomorphe, Burkartia, Catananche, Celmisia, Centaurea, Chamaechaenactis, Chuquiraga, Cichorium, Dubautia, Erigeron, Euchiton, Euryops, Ewartia, Gamochaeta, Haastia, Helichrysum, Heterotheca, Hippolytia, Jurinella, Lagenocypsela, Launaea, Leontopodium, Leucogenes, Lucilia, Mniodes, Nardophyllum, Nassauvia, Pentacalia, Psephellus, Pterygopappus, Raoulia, Raouliopsis, Saussurea, Scorzonera, Senecio, Sinoleontopodium, Townsendia, Waldheimia, Werneria, Xenophyllum, Youngia*
Boraginaceae	13	6	0	0	1	*Alkanna, Amblynotus, Chionocharis, Eritrichium, Myosotis*
Boryaceae	0	5	0	0	0	*Borya*
Brassicaceae	60	20	4	3	13	*Alyssum, Arabis, Aubrieta, Baimashania, Borodinia, Brayopsis, Dactylocardamum, Degenia, Delpinophytum, Draba, Eudema, Lepidium, Lithodraba, Onuris, Petrocallis, Physaria, Physoptychis, Ptilotrichum, Shangrilaia, Solms-laubachia, Subularia, Thlaspi, Vella, Xerodraba, Zilla*
Bromeliaceae	0	0	0	0	2	*Deuterocohnia*
Cactaceae	0	27	0	0	1	*Austrocylindropuntia, Copiapoa, Cumulopuntia, Echinocereus, Epithelantha, Ferocactus, Gymnocalycium, Maihueniopsis, Mammillaria, Opuntia, Tunilla*
Calceolariaceae	1	1	1	0	2	*Calceolaria*
Campanulaceae	8	0	2	0	2	*Asyneuma, Campanula, Edraianthus, Lysipomia, Muehlbergella, Wahlenbergia*
Caprifoliaceae	7	2	3	3	0	*Aretiastrum, Phyllactis, Pterocephalus, Valeriana*
Caryophyllaceae	77	46	27	1	14	*Acanthophyllum, Arenaria, Bolanthus, Colobanthus, Dianthus, Eremogone, Gypsophila, Minuartia, Mniarum, Paronychia, Philippiella, Pycnophyllopsis, Pycnophyllum, Reicheella, Sagina, Saponaria, Scleranthus, Silene, Stellaria, Thylacospermum*
Celastraceae	0	0	0	0	1	*Stackhousia*
Centrolepidaceae	8	0	0	0	0	*Centrolepis, Gaimardia*

Convolvulaceae	3	1	0	0	3	*Convolvulus*
Crassulaceae	1	0	0	5	0	*Crassula, Sempervivum*
Cyperaceae	16	5	0	0	5	*Carex, Carpha, Oreobolus, Phylloscirpus, Rhynchospora, Schoenus, Zameioscirpus*
Diapensiaceae	1	0	1	0	0	*Diapensia*
Dilleniaceae	0	0	0	4	0	*Hibbertia*
Ericaceae	3	3	1	2	1	*Andersonia, Disterigma, Rhododendron, Dracophyllum, Pentachondra*
Eriocaulaceae	17	0	0	0	1	*Eriocaulon, Paepalanthus*
Euphorbiaceae	1	9	0	0	0	*Euphorbia*
Fabaceae	9	116	0	17	4	*Acacia, Adesmia, Anarthrophyllum, Anthyllis, Astracantha, Astragalus, Carthamus, Chesneya, Cicer, Cousinia, Cytisus, Echinospartum, Erinacea, Eutaxia, Genista, Lotus, Lupinus, Onobrychis, Orophaca, Oxytropis, Sarcopoterium*
Frankeniaceae	0	1	0	2	1	*Frankenia*
Gentianaceae	2	2	2	0	0	*Gentiana, Gentianella, Halenia*
Geraniaceae	2	1	1	1	1	*Geranium*
Goodeniaceae	2	1	0	0	1	*Lechenaultia, Scaevola*
Iridaceae	1	0	0	0	0	*Tapeinia*
Juncaceae	4	1	0	0	9	*Distichia, Juncus, Luzula, Oxychloe, Patosia*
Lamiaceae	0	2	0	2	2	*Ajuga, Hedeoma, Thymus, Ziziphora*
Linaceae	1	1	0	0	0	*Linum*
Loasaceae	0	1	0	0	0	*Loasa*
Loganiaceae	1	0	0	0	1	*Mitrasacme*
Malvaceae	28	1	0	0	1	*Nototriche*
Montiaceae	2	0	1	0	0	*Hectorella, Lyallia, Phemeranthus*
Oleaceae	0	2	0	0	0	*Jasminum*
Oxalidaceae	4	2	0	0	0	*Oxalis*
Papaveraceae	0	2	0	0	0	*Corydalis*
Plantaginaceae	6	1	7	1	1	*Globularia, Plantago, Veronica*
Plumbaginaceae	14	59	2	3	7	*Acantholimon, Armeria, Limonium*

Poaceae	16	0	0	0	0	*Aciachne, Agrostis, Calamagrostis, Deschampsia, Ehrharta, Kobresia, Poa, Sporobolus, Rytidosperma*
Polemoniaceae	3	2	1	1	1	*Gilia, Phlox*
Polygonaceae	0	1	0	0	1	*Eriogonum*
Portulacaceae	1	0	4	0	0	*Calandrinia*
Primulaceae	62	7	3	0	7	*Androsace, Dionysia, Primula, Vitaliana*
Ranunculaceae	1	0	0	0	3	*Paraquilegia, Psychrophila, Ranunculus*
Rhamnaceae	0	0	0	0	1	*Rhamnus*
Rosaceae	9	6	0	8	4	*Acaena, Ivesia, Petrophytum, Potentilla, Kelseya, Sibbaldia*
Rubiaceae	5	6	3	2	5	*Asperula, Galium, Oldenlandia, Oreopolus, Rubia*
Salicaceae	0	0	0	0	1	*Salix*
Saxifragaceae	97	11	4	4	7	*Saxifraga, Saxifragella*
Scrophulariaceae	0	1	0	0	0	*Verbascum*
Solanaceae	12	0	0	0	5	*Benthamiella, Combera, Fabiana, Pantacantha, Petunia*
Stylidiaceae	3	1	2	0	2	*Donatia, Phyllachne, Stylidium*
Thymelaeaceae	1	2	0	0	4	*Drapetes, Kelleria, Pimelea*
Verbenaceae	5	4	0	4	2	*Junellia*
Violaceae	2	0	2	0	0	*Viola*
Xyridaceae	0	1	0	0	0	*Xyris*
62 families	587	398	91	90	145	273 genera

Table 3. Angiosperm families and genera that contain cushion or mat species. For 62 Angiosperm families, the number of species it contains in the three following types is presented: dome-shaped cushions, cushions (dome-shaped or flat) and cushions and mats. The last column gives the genera in each family that contain either cushions or mats. In the last row, the total for each category is given. Asteraceae, Caryophyllaceae, Fabaceae and Saxifragaceae stand out as the families that contain the largest numbers of cushion species.

CONTINENT	HEMISPHERICAL CUSHIONS		FLAT CUSHIONS		OTHER	TOTAL	PROPORTION OF ALL SPECIES IN THE CATALOGUE
	COMPACT	NON COMPACT	COMPACT	NON COMPACT			
North America	35	25	8	4	15	87	6.6%
South America	166	58	51	28	48	351	26.8%
Europe	80	64	17	10	17	188	14.3%
Africa	15	26	0	9	6	56	4.3%
Asia tropical	76	24	4	6	12	122	9.3%
Asia temperate	197	221	10	26	33	487	37.1%
Australasia	72	16	6	13	29	136	10.4%
Antarctic	8	1	2	0	3	14	1.1%

Table 4. Distribution of cushion plants in the continents, on the basis of the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001). The sum of all proportions exceeds 100% since some species occur on several continents.

ARTICLE 4.2

HISTOIRE DE LA FORME DE VIE EN COUSSIN CHEZ LES ANGIOSPERMES

EVOLUTION OF THE CUSHION LIFE FORM IN ANGIOSPERMS

Florian C. Boucher, Sébastien Lavergne, Philippe Choler & Serge Aubert

SUMMARY

- Cushion-forming species are present in all alpine and arctic ecosystems worldwide. They are key members of these ecosystems since they have important engineering roles, enabling the establishment of other species. Hundreds of species of cushions exist, that belong to very diverse Angiosperms lineages, but their history remains poorly known.
- Here we investigate the evolutionary and biogeographic history of cushions in Angiosperms using a list of all species that bear this life form, as well as phylogenetic, climatic and biogeographic information. Our aim is to document the extent of this evolutionary convergence and identify potential historic, environmental and biogeographic factors that enabled its evolution.
- We show that cushions appeared at the very least 41 times, and that they are clustered in several parts of the Angiosperms phylogeny. Cushions are found in families able to live in cold and dry environments, confirming that they are an adaptation to alpine and arctic environments. Finally, we show that the main centers of cushion diversity may have had different roles. While most cushions in the Himalayas, the Andes or New Zealand may have originated *in situ*, Patagonia seems to be a hub that enabled many cushions to migrate between South America and Austral regions.
- We conclude that the cushion life form is an impressive example of a convergent key innovation, which has enabled the occupancy of alpine and arctic environments. These results have implications for our understanding of the origins of cold biomes, which are among the most threatened today.

INTRODUCTION

Cushion plants are emblematic members of alpine and arctic floras worldwide. They contain some of the species of angiosperms that occupy the coldest habitats on Earth, having been recorded above 6,000m in the Himalayas (e.g. members of the genera *Arenaria* and *Stellaria*, Grabherr et al., 1995) and above 4,200m in the Alps (e.g. *Androsace helvetica*, Körner, 2011), while *Colobanthus quitensis* is one of the few Angiosperms native of the Antarctic continent (Rudolph, 1965). Hundreds of species of cushions exist, which are widespread across Angiosperms and are distributed in all continents of Earth (Aubert et al., In prep.). They are perennial plants characterized by a dense branching, which usually grow very slowly and are thus extremely long-lived organisms (e.g. Morris & Doak, 1998).

Cushions have attracted botanists since the time of the firsts naturalist explorations that explored the different mountainous regions of the world (Weddel, 1857; Cockayne, 1912; Hauri & Schröter, 1914). Community ecology has also extensively studied cushions for their important ecological role in alpine and arctic environments, where they are frequently described as ecosystem engineers (Badano et al., 2006). Indeed, they often act as foundation species that facilitate the establishment of microbes (Roy et al., 2013) and of other plant species (Reid et al., 2010; Schöb et al., 2012), thereby increasing plant diversity (Butterfield et al., 2013).

Given that cushions are important members of arctic and alpine floras, it has long been hypothesized that they represent an adaptation to cold conditions (Raunkiaer, 1934). This has been confirmed in experimental settings, where leaves, stems and roots of several cushion species appeared to be resistant to frost damage up to -15°C (Larcher et al., 2010). A comparative study of the genus *Androsace* also showed that cushion species were adapted to colder temperatures than their non-cushion forming relatives (Boucher et al., 2012). However, it is also possible that the cushion life form is an adaptation to drought, since some species of cushions inhabit cold deserts. For example, *Thylacospermum caespitosum* is found places of Eastern Ladakh (trans-Himalaya) where precipitation is less than 100mm/year (de Bello et al., 2011). Importantly, also some level of plasticity exists (Spomer, 1964), the cushion life form is largely inherited genetically, as shown by the many rock gardens that host cushions plants in environments that are very different from their native ones.

The diversity of cushion species also poses question. Indeed, this life form seems to be a large evolutionary convergence, which appeared in very different sections of the Angiosperms and in different parts of the world (Aubert et al., In prep.). This has to have happened relatively recently in the history of Angiosperms since alpine and arctic environments, that cushions principally occupy, are relatively young

(Fine & Ree, 2006). Furthermore, these cold environments are generally less prone to diversification than the tropics (Wright et al., 2006). Contrary to other groups of plants like grasses whose history is well understood (e.g. Grass Phylogeny Working G., 2012), little is known on cushion species. Such knowledge is needed given the importance of cushions in structuring alpine and arctic ecosystems.

In this article we combine botanical, phylogenetic, climatic and geographic information to investigate the history of the cushion life form in Angiosperms. We first ask how widespread is this evolutionary convergence and estimate the minimum number of independent appearances of the cushion life form in Angiosperms. Then, to investigate the more in the details the history of cushions, we ask whether cushions appeared at random in the Angiosperm tree or if they are restricted to specific clades. Finally, we try to unravel the drivers of the evolution of the cushion life form and address the following questions: (i) is cold and/or drought responsible for the appearance of the cushion life form? ; and (ii) have some regions of the world been more prone to cushion evolution, and if yes why?

MATERIAL AND METHODS

List of cushion species and phylogenetic relationships

The cushion species inventory used in this analysis is compiled from the database of Aubert et al. (In prep., www.cushionplants.org). This list of Angiosperm species bearing the cushion life form is the most exhaustive to date and has been compiled using information form various sources including floras, regional checklists, scientific articles and monographs (see Aubert et al., In prep.). Information on the morphology of each species is available, including its shape and compactness. The database includes 1311 species that are distributed on all continents in the World and belong to 62 different families of Angiosperms. Family names in this database as well as in this article follow the APGIII nomenclature (Stevens, 2001+).
From this database we only retained the 678 species that have a compact morphology, being either dome-shaped (e.g. *Androsace helvetica*) or flat (e.g. *Silene acaulis*). The definition of cushions used in this article is thus a rather strict one, excluding loose cushions (e.g. *Saxifraga oppositifolia*) or mats (e.g. *Raoulia australis*). These cushions belong to 44 different Angiosperm families and 156 genera; they represent 0.25% of all Angiosperm species (c.a. 270,000 species, Vamosi & Vamosi, 2010). They span both monocots and eudicots (see Fig. 1). Our choice of including only compact cushions was primarily motivated by the fact that the information on compactness was very consistent and almost always given in the sources that were used for building the database (Aubert et al., In prep.). Furthermore, it has been shown that the compact morphology is genetically

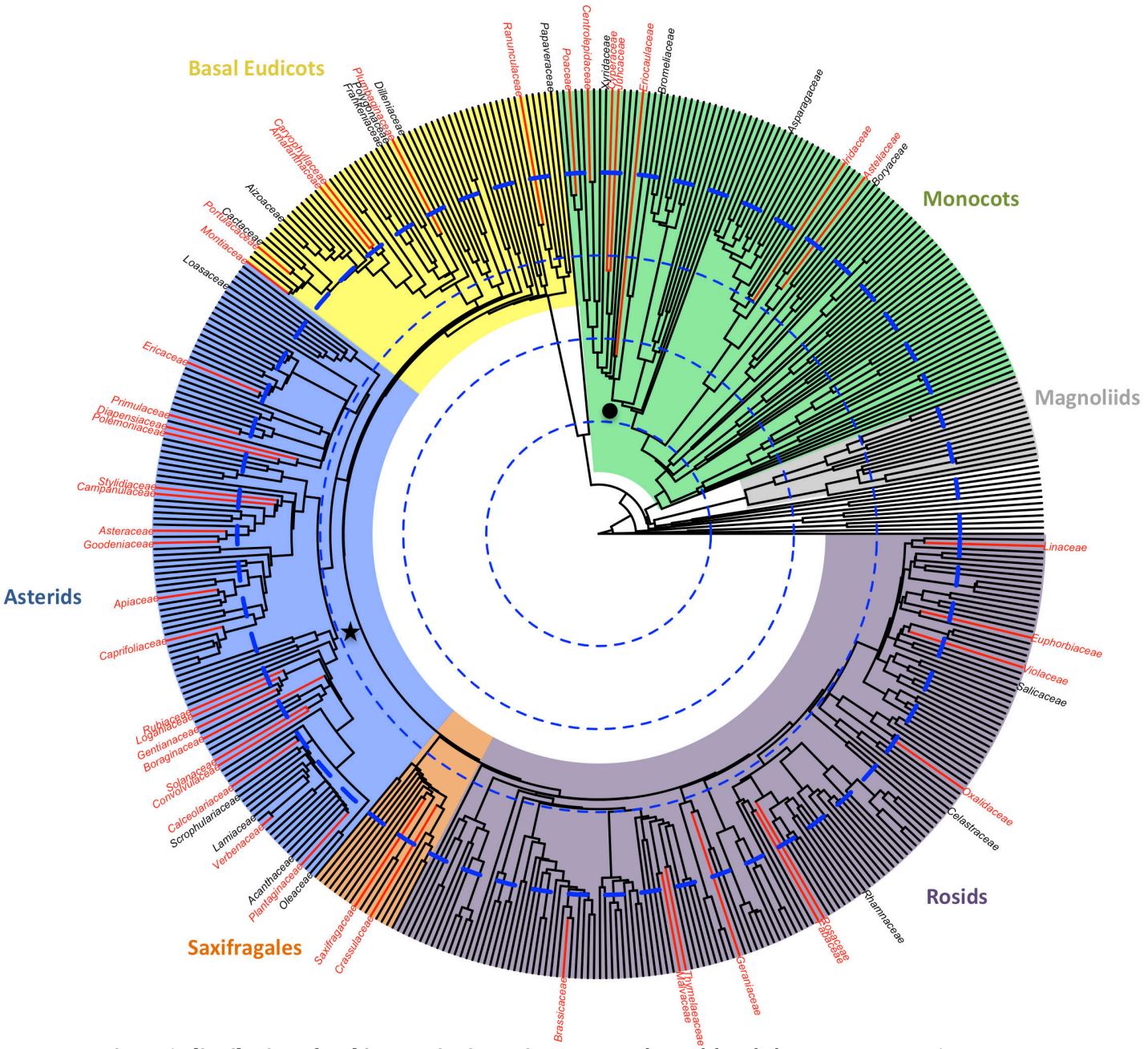

Figure 1: distribution of cushion species in Angiosperms. Each tip of this phylogenetic tree is an Angiosperm family (Fiz-Palacios et al. 2011) and major groups according to the APG III system are underlined with different colors. Red terminal branches and tips show the 44 families that contain species of compact cushions that are included in our study. Families in black are other Angiosperm families that contain non-compact cushions or mats. Blue circles show slices of 50Mya, measured form the present. The widest circle, at -50Mya indicates the approximate time of appearing of cold biomes on Earth, before which cushions very likely did not appear. The black circle and the black star respectively indicate the root of Poales and of the euasterid I clade, which contain the highest density of families bearing cushions.

inherited, whereas this seems to be more plastic in lax cushions or mats (Spomer, 1964).

In order to study the history of the cushion life form in Angiosperms, we needed phylogenetic information. As a detailed species-level phylogeny is not available for Angiosperms, we used the family-level phylogeny of land plants of Fiz-Palacios et al. (2011), which includes the 706 currently accepted families of land plants. This tree was built using both plastid (rbcL, atpB and rps4) and nuclear ribosomal genes (18S and 26S) and inference was made using maximum likelihood analyses. Divergence times were estimated using penalized

likelihood and the tree was calibrated using multiple fossils. We then trimmed the tree of land plants to retain only the 453 families of Angiosperms. *Amborella trichopoda* was used as an outgroup to root this tree. This tree of Angiosperm families is rather well resolved since there are only five polytomies (see Fig. 1); its crown age is estimated to be 267.6 Mya. The age of Angiosperms has been largely discussed in the literature, and this estimate should be interpreted with caution as it is much older than previously thought (Wikstrom et al., 2001; Davies et al., 2004; Bell et al., 2010). However, in this tree the age of eudicots (to which 37 of the 44 families containing compact cushions belong) was calibrated to 121 Mya, in agreement with other studies. In the following of this article, all divergence times that are given follow Fiz-Palacios et al. (2011).

Appearing of the cushion life form in Angiosperms

Given that the cushion life form is likely to have evolved several times independently in many families (it has even been shown to have appeared two times in a single genus, Androsace s.l., Boucher et al., 2012), the phylogenetic tree resolved at the family level that we used would not allow to go into the finest details of the evolution of the cushion life form. We thus decided to record the minimum number of independent appearings of this key innovation in Angiosperms. To do so, we coded each Angiosperm family as having at least one species of cushion (1) or not (0) and estimated ancestral values of this binary character in the Angiosperm tree using parsimony. This was done by setting all branch lengths to unity in the Angiosperm tree and then running an ancestral state reconstruction by maximum likelihood using the 'ace' function in the ape package (Paradis et al., 2004). Given that the alpine regions to which cushions are likely adapted (see Results) did not appear on Earth before -50Ma, when the orogeny of the Himalayas started (Yin & Harrison, 2000) and that boreal biomes appeared even latter, in the Miocene (Fine & Ree, 2006), we made the hypothesis that cushions did not appear before -50Ma. The number of independent appearings that happened after -50Ma was then recorded by counting them on the Angiosperm tree.

Distribution of cushion species in the Angiosperms tree

Cushions are widely distributed in the Angiosperm tree and belong to very different families (e.g. Poaceae, Iridaceae, Euphorbiaceae and Rosaceae, see Fig. 1), suggesting that this trait is not too much constrained by the developmental or architectural characteristics of plants. One could even wonder whether this trait is randomly distributed among Angiosperms, which would indicate that it is not at all depending on pre-existing biological characteristics in the families where it occurs. On the contrary, detecting clustering of families bearing cushions among all

Angiosperm families would not imply that the evolution of the cushion life form depends on pre-existing traits: it could just be that families that have managed to occupy cold climates (to which cushions are adapted, see Results) are clustered in the Angiosperms tree.

To test the specific hypothesis that cushions are clustered even among families able to occupy cold environments, we measured the mean pairwise phylogenetic distance (MPD, (Webb et al., 2002)) between two families harboring cushions To provide a null expectation for this index, we used a randomization approach: the index was calculated across 9,999 random resamples of families in the tree (same number of families that those containing cushion species) to build null distributions. The observed MPD values among families bearing cushions were then compared to the null distributions to test whether families bearing cushions are clustered (distances between two families bearing cushions smaller than randomized distances) and to obtain p-values for these tests. As cushions do not appear in the most basal groups of Angiosperms (i.e. Nymphaeales, Austrobaileyales, Magnoliids, Chloranthales, Acorales, Alismatales and Petrosaviales) and because that would increase the randomized values, the tree of families was first trimmed to the smallest monophyletic tree containing all cushion species. Three families that bear cushions but that could share it from a common ancestor with other families (see Results) were also trimmed from the tree, these were: Amaranthaceae, Goodenianceae, and Montiaceae. The phylogenetic distance between two families was measured as the time since their divergence.

To tease apart the clustering that could be due to the climatic tolerances of the families, a subtree containing only the families able to live in environments having a sum of growing degree days <1000°C was built. We then applied the same randomization procedure across those 'cold tolerant' families to assess whether families having cushions are closer phylogenetically than expected by chance.

Finally, as clustering at the level of all Angiosperms could result from small clusters in some parts of the tree, we also tested whether families bearing cushions were clustered in several subgroups of Angiosperms.

Climatic drivers of the evolution of the cushion life form

To estimate the relative importance of cold and drought in driving the evolution of the cushion life form, we calculated the climate experienced by a subset of 257 Angiosperm families. For these, distribution grids covering the entire Earth at a resolution of 10 arc-minutes were obtained from the UNEP World Conservation Monitoring Centre (www. unep-wcmc.org). On each point of this grid, the sum of growing-degree days above 5°C (hereafter GDD5, CRU dataset) and the ratio of actual to potential evapotranspiration (hereafter AETPET, Thuiller et al., 2005) were sampled. GDD5 is

an important driver of plant phenology and biomass production and may be a better descriptor of thermic stress in plants than mean annual temperature. Given its importance for many aspects of plant physiology (Stephenson, 1990), AETPET was used to characterize hydric stress. For each family whose distribution was available, we recorded the distribution of GDD5 and AETPET over its range. These distributions were weighted by the area of the different pixels (i.e. taking into account that pixels at high latitudes are in reality smaller than pixels at low latitudes). The 10% quantiles of these distributions were used to characterize the extremes of each family on the cold and drought gradients.

Finally, we used generalized estimating equations to study the link between the presence of cushions in a family and its climatic extremes while controlling for the possible phylogenetic correlation between families. In this model, the presence of at least one species of cushion in a family was taken as the binary response (i.e. cushions or not) using a binomial link. The cold and dry extremes of each family were the explanatory variables. Both cold and dry extremes of the 257 families were transformed in order to have mean=0 and sd=1, so that the effects of both variables could be compared. We used two structures for the variance-covariance structure of residuals in this model: (i) one where it is given by phylogenetic relationships between families (i.e. covariance proportional to evolutionary time shared by two families before their divergence) and (ii) a model without phylogenetic correlation. These two alternative models were compared using the quasi-likelihood information criterion (Pan, 2001).

Biogeographic patterns of cushion diversity

To investigate the geographic distribution of cushion plants worldwide, we used the World Geographical Scheme for Recording Plant Distributions (Brummitt, 2001). This scheme defines different spatial scales, ranging from continents to countries or even provinces. The finest scale that could be documented for all 678 species included in our study was the level 3 classification that divides landmasses of the globe into 369 regions. We acknowledge that this classification is not ideal since some regions of the world (e.g. Kazakhstan) are less finely divided than others (e.g. Albania), but it is the most precise that one can achieve on a large sample of plant species. Both the literature and the Global Biodiversity Information Facility (www.gbif.org) were used to document the distribution of every species (see (Aubert et al., In prep.) for more details).

In order to identify the areas of the globe that contain the highest densities of cushion species, we measured the area of mountains (in km^2) each of the 369 regions using a ruggedness threshold of >200m of difference in altitude with a 2.5 arc-minute cell (0.5 arc-minute resolution, see Körner et al., 2011). We also calculated the area of

'cold' environments in each region (i.e. GDD5<3,000°C). These two variables are hereafter referred to as 'rugged' and 'cold' areas; they were chosen instead of the total area of each region because cushions are primarily found in arctic and alpine regions. The number of cushion species in one area as well as the rugged or cold area of this region was then used to build species-area relationships. Power functions were used to fit these curves, as these are the parametric functions that usually best describe the relationship between species richness and area (Gleason, 1922). 'Hotspots' of cushion species were then identified as the largest positive outliers (i.e. areas that depart the most from the fitted curve). To examine the effects of drought on the distribution of cushion species, we calculated the mean aridity (total annual precipitation divided by potential evapotranspiration) in each region and examined the relationship between residuals of the species-area relationships and aridity.

Cushion species in a region either result from in situ diversification or from immigration from another region. To provide a first look at that question, in the top 15 hotspots of cushion species, we calculated the number of cushion genera and families as well as the proportion of cushions that are endemic to the region. We expect that regions that have many species of cushions belonging to relatively few genera and families might have been places where cushions diversified extensively. On the opposite, regions with a relatively high number of genera and families with cushions might be preferred routes of migration for cushions. Finally, a high proportion of cushions endemic to a region would indicate that this region is isolated from other centers of cushion diversity.

All analyzes were run in R (R Development Core Team, 2012), using packages ape (Paradis et al., 2004), picante (Kembel et al., 2010), and raster.

RESULTS

Appearing and distribution of cushion species in the Angiosperms tree

The parsimonious ancestral character estimation yielded a minimum of 28 independent appearings of the cushion life form in Angiosperms. However, when considering that the cushion life form cannot have appeared before -50Myr, 41 independent appearings are recorded. Indeed, only three couples of Angiosperm families may share a common origin of cushions that is more recent than -50Ma: Asteraceae and Goodeniaceae, which diverged 43.6Ma ago, Montiaceae and Portulacaceae, which diverged 34.4 Mya ago and Caryophyllaceae and Amaranthaceae, which diverged 47.1Ma ago. In all other cases cushions appeared either in terminal branches (i.e. inside families) or before -50 Mya (see Fig. S1). Note that the age of Angiosperms used in this study (i.e. -267.6 Mya) is not very problematic. Indeed, it does not affect the age of all eudicots, which has been calibrated to -121 Mya. In monocots,

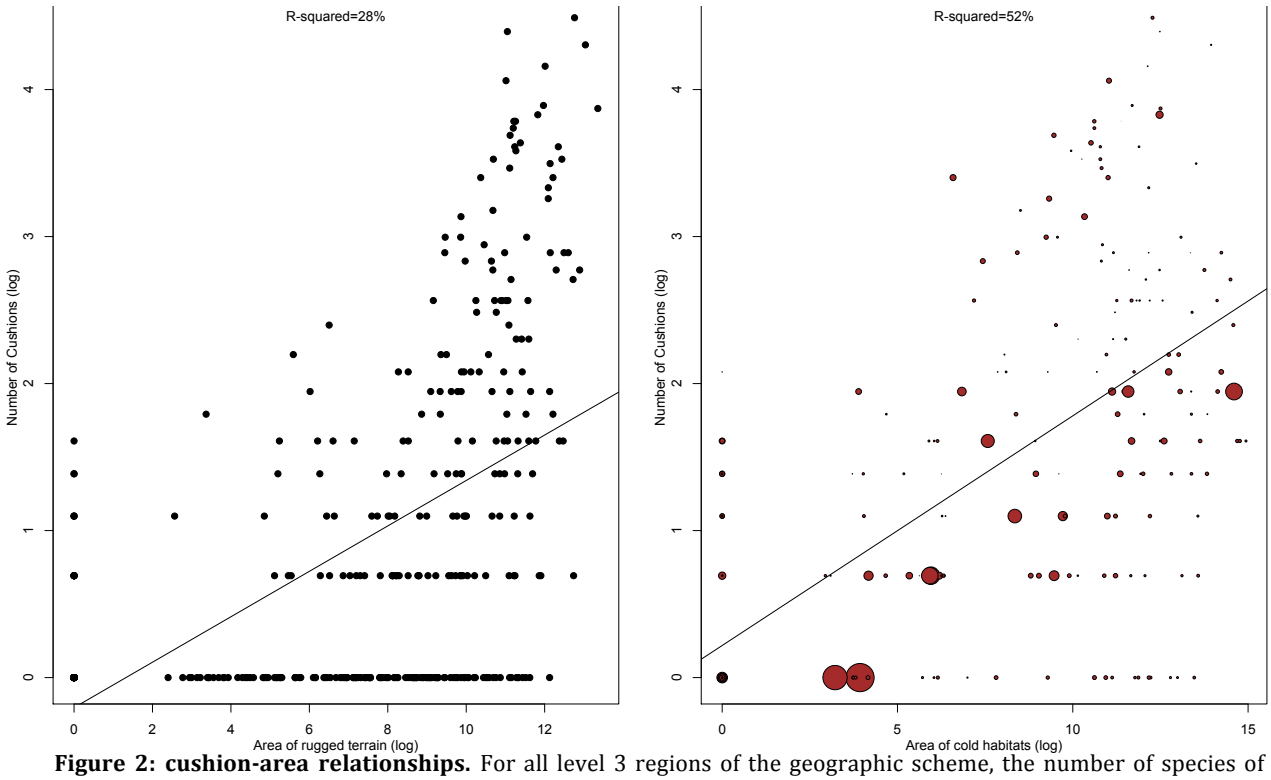

Figure 2: cushion-area relationships. For all level 3 regions of the geographic scheme, the number of species of cushions was compared to the area of rugged terrain in each region (left plot) and to the area where the sum of growing-degree-days above 5°C is less than 3,000 (right plot). Both plots are shown on a log-log scale and show a triangular relationship: while the number of cushions generally increases with area, some large areas have few cushions. On the right plot, the size of each point is inversely proportional to the average aridity in the corresponding region: positive outliers are the driest regions.

the two families that could eventually share a common origin of cushions and diverged most recently are Cyperaceae and Juncaceae, which have been estimated to have diverged before -50 Mya using other calibration procedures (Bremer, 2002).

Families bearing species of cushions were significantly clustered among Angiosperms (Z-score=-2.12, p=0.018 for MPD) and on average diverged from the closest family bearing cushions 86 Myr ago. This clustering was also significant even when considering only families that are cold tolerant (Z-score=-1.80, p=0.043). However, this was mainly due to a cluster in monocots (Z-score=-2.98, p=0.012), with five out of seven families of monocots having species in cushion belonging to Poales. In contrast, clustering was not significant in asterids (Z-score=-0.43, p=0.292), and families bearing cushions were even over dispersed in rosids (Z-score=0.61, p=0.281).

Climatic and biogeographic drivers of the evolution of the cushion life form

The best model for the link between the presence of cushions in one family and its climatic extremes was a model with no phylogenetic signal in the residuals ($QIC_{phylogeny}$=178.8, while $QIC_{no\ phylogeny}$=171.5). In this model, families having cold (p<1e-5) and dry (p=0.005) climatic extremes had a significantly higher probability of bearing cushion species than other families. However, the effect of cold was 2.3 times larger than that of drought (estimated regression coefficients being -1.76 and -0.76, respectively). In the model where residuals co-varied according to the

phylogeny, only cold had a significant effect ($p=0.007$), while drought had not ($p=0.14$).

The number of cushions exhibited a triangular relationship with both rugged and cold areas of each region: there was a positive relationship between the number of cushion species and area ($p<2e\text{-}16$ in both cases), but many regions having large areas of rugged and/or cold climate had very few cushion species (see Fig. 2). The cold area was a better predictor of the number of cushions than the area of rugged terrain ($R^2=52\%$ and $R^2=38\%$, respectively). Residuals of the relation between the number of cushions and cold area were positively correlated with the average aridity of each region ($p=0.013$, see Fig. 2), but no relation was found for the area of rugged terrain ($p=0.882$). Although not in the same order, both analyses identified the same top 15 hotspots of cushion richness (see Table 1), the five firsts being in both cases Southern and Northwestern Argentina, Peru, the Southern island of New Zealand, and Tibet. Among these 15 regions that are exceptionally cushion-rich, the Southern island of New Zealand was the one that had the highest proportion of endemic cushions (63%), followed by Peru (36%) and Southern Argentina (30%).

Region	Species	Families	Genera	Endemics
Argentina South	80	23	40	30%
Peru	88	17	31	36%
New Zealand South	57	14	23	63%
Argentina Northwest	63	16	27	8%
Tibet	73	8	15	18%
Chile North	43	14	21	2%
Nepal	43	8	12	16%
Italy	41	8	12	14%
Bolivia	48	13	24	10%
Ecuador	39	13	19	26%
Chile South	45	18	29	4%
France	33	8	11	3%
Chile Central	36	17	23	0%
East Himalaya	37	7	11	8%
Spain	35	9	13	23%

Table 1: composition of the 15 most cushion-rich regions in the world. Regions are ranked in decreasing order according to the number of species of cushion per area of rugged terrain (i.e. the first is the hottest hotspot). For each region, the number of species of cushions, as well as the number of families and genera they belong, is given. The last column presents the proportion of cushions that are endemic to each region.

DISCUSSION

The 678 species of compact cushions that we identified belong to 44 Angiosperm families, which differ a lot in their number of cushion species. Families that contain the most cushion species are Caryophyllaceae (104 sp.), Saxifragaceae (101 sp.), Primulaceae (65 sp.), Brassicaceae (64 sp.) and Asteraceae (63 sp.). On the contrary, only one species of cushion is present in Crassulaceae, Euphorbiaceae, Iridaceae, Linaceae, Loganiaceae, Ranunculaceae and Thymeleaceae. However, most of the cushion rich families are simply large families (e.g. 23600 sp. in Asteraceae, 3710 sp. in Brassicaceae, 2590 sp. in Primulaceae and 2200 sp. in Caryophyllaceae) and the proportion of cushions in Asteraceae is similar to the proportion of cushions in all Angiosperms (i.e. 0.25%). Families containing the highest proportions of

cushions are distributed in different major angiosperm clades: Saxifragaceae (27.3%) belong to Saxifragales, Centrolepidaceae (22.9%) to monocots, Portulacaceae (12.5%) to basal eudicots and Diapensiaceae (11.1%) to asterids. In euasterids I, where the concentration of families bearing cushions is relatively high (9 out of 41 families), all families have a rather low proportion of cushions (less than 1%).

An impressive example of evolutionary convergence among Angiosperms

Compact cushions are found in all major Angiosperm groups except the most basal lineages (Fig. 1). Our parsimonious estimation yielded a minimum of 41 independent appearings of the cushion life form in Angiosperms, consisting of 7 appearings in monocots, 4 in basal eudicots, 18 in asterids, 2 in Saxifragales and 10 in rosids (Fig SX). This number is already very high and competes with the number of independent appearings of C4 photosynthesis in plants (i.e. 45, (Sage, 2004). However, this estimation is very conservative and the real number of independent appearings of the cushion life form may be much higher. Indeed, it is very likely that the cushion life form evolved independently in all families where it is present and even repeatedly inside families. For example in Primulaceae, cushions have been shown to evolve at least twice in the genus Androsace (Boucher et al., 2012). But cushions also exist in Dionysia and Primula, two genera that are not closely related (Yesson et al., 2009). It is thus likely that the cushion life form evolved at least four times independently in Primulaceae alone. If this kind of scenario with multiple appearings inside families (or even inside genera) were to be the norm rather than the exception, the true number of appearings of the cushion life form could largely exceed one hundred. The fact that the proportion of cushions in Angiosperm families is relatively low (maximum 27.3% and only 14 families with more than 1% of cushions) also suggests that the cushion life form may not be an ancestral character in most families. Anyway, even our very conservative estimate shows that the cushion life form is one of the most widespread evolutionary convergences in Angiosperms.

Clustering of cushions in Angiosperms suggests physiological prerequisites

Given the frequency of this convergence and the fact that it evolved in very different angiosperm clades, the cushion life forms seems to be a morphological character that is very easy to evolve. We however found that cushions were not distributed at random in Angiosperms and that families containing cushion species were significantly clustered, even among families that occupy cold habitats. For example, three couples of sister families both bear cushion species: Cyperaceae and Juncaceae (monocots); Amaranthaceae and Caryophyllaceae (basal eudicots); Convolvulaceae and Solanaceae (asterids). The highest concentration of cushions is

found in Poales, where 5 out of 16 families bear cushions (i.e. Centrolepidaceae, Cyperaceae, Eriocaulaceae, Juncaceae, and Poaceae), while two other families (i.e. Bromeliaceae and Xyridaceae) contain some loose cushions or mats (Fig. 1). Asterids also contain a rather high proportion of families with cushions and these are most densely concentrated in euasterids I, where 9 of the 41 families contain compact cushions (Fig. 1). The fact that families bearing cushions are on average more closely related between them than to other families suggests that some characteristics might be prerequisites for the cushion life form to appear. An obvious character that is needed for the cushion life form to evolve is the presence of ramifications, but this trait alone is unlikely to create the degree of clustering observed since the vast majority of Angiosperm families possess ramifications. More importantly, the formation of the cushion habit requires dense branching and short internodes. Auxin and cytokine are no doubt important components of these two developmental patterns (Zhao, 2010) and their role in controlling the cushion habit deserve more attention. Moreover, strigolactones, a class of recently described hormones, have been shown to be inhibitors of branching (Umehara et al., 2008) and evidence suggests that some of the genes controlling their synthesis are conserved across large groups of plants (Johnson et al., 2006). Further work on the hormonal drivers of the cushion life form and their genetic basis is thus needed to identify the physiological enablers of the evolution of the cushion life form.

An adaptive response to cold and dry environments

Botanists have long recognized that cushions are numerous in alpine and arctic regions around the world (Raunkiaer, 1934) and thus hypothesized that it represents an adaptation to these environments. Using our extensive dataset, we verified that cushion species are primarily found in families that occur in very cold conditions, and to a lesser extent in families occurring in dry conditions (Fig. XX). This confirms results of studies that have shown that the cushion life form was a key innovation that enabled the occupancy of cold environments at a finer phylogenetic scale (Boucher et al., 2012) or even in experimental settings (Larcher et al., 2010). Together, this indicates that the cushion life form has been selected under cold, and to a lesser extent dry climatic conditions. It thus represents an adaptive convergence of many angiosperms lineages to arctico-alpine conditions, which phylogenetic and geographic extents are extremely large.

However, the cushion life form is not the only one of plants living in cold places. Indeed, the angiosperm species that has been found in the coldest place of earth is *Saxifraga oppositifolia* (Körner, 2011), a species that grows in flat and lax mats. One of the other arctic champions, *Papaver*

radicatum, does not even form mats but a single rosette.

Potential cradles and hubs of cushion diversity

Cushion species are largely distributed in arctic and alpine areas of all continents on Earth. However, regions differ in the number of cushions that they possess. Indeed, 217 species of compact cushions can be found in South America and 207 species in temperate Asia. In contrast, only 97 species inhabit Europe, 58 occupy Australasia and 43 are distributed in North America. We found that the number of cushion species generally increased with the area of cold environments in each region and also with the aridity of the region, thereby confirming that cushions are adapted to cold deserts. When correcting for the effect of area, we found that the regions of the world with the highest concentrations of cushion species were Patagonia, the Central and Southern Andes (Ecuador, Peru, Bolivia, Chile, and Northwestern Argentina), the Himalayas (Tibet, Nepal, and Eastern Himalayas), the Southern island of New Zealand, the Southern Alps (Italy and France) and the Pyrenees. In contrast, arctic regions or the Rocky Mountains are not exceptionally cushion-rich.

These regions that host many cushion species may however have had different biogeographic histories. Among these main centers of cushion diversity, Tibet, Nepal, and the Eastern Himalayas have a high number of cushions but these belong to relatively few distinct genera and families, which tends to indicate that these regions might have been places of extensive diversification for cushions. This is corroborated by the fact that the Himalayas is the oldest mountain range on Earth, thus offering more time for cushion diversity to grow. The situation is rather similar in the Alps and the Pyrenees, although fewer cushion species occupy these regions, probably because mountains are younger and occupy less area in these regions. All these regions of the southern mountain ranges of Eurasia have rather low levels of cushion endemism, indicating that migration along these mountain ranges might be rather frequent.

In the Andes, more families and genera containing cushions can be found, which might indicate that migration along this mountain range is an important contributor to the richness of cushions in the Andes. The average number of species of cushions per genus is also lower than in Eurasia, which is an agreement with the fact that altitudes above 2,000m are very recent in the Andes (Hartley, 2003). While Ecuador and Peru contain a rather high percentage of endemic cushions (respectively 26% and 36%), regions south of Peru (i.e. Bolivia, North and Central Chile and Northwestern Argentina) seem to be highly connected since they have very few endemics.

Patagonia (i.e. Southern Chile and Southern Argentina) has a relatively high number of different genera and families but few species of cushions per genus. This could be due to

its rather young history that allowed little time for diversification to take place (Le Roux, 2012) but also probably reflects the fact that Patagonia has for long been a region connecting landmasses of the temperate Southern Hemisphere (i.e. Austral Africa, Australia, New Zealand, sub Antarctic islands, and the Antarctic continent) to South America (Crisp et al., 2009).

Finally, the case of New Zealand is singular because it bears both traces of connections with other Austral regions and of isolation. For example, the Southern island of New Zealand shares seven genera containing cushions with Patagonia: one of them is widespread (*Oreobolus*), others are largely distributed in the southern Hemisphere (*Astelia*, *Abrotanella*, *Colobanthus*, *Gaimardia*), while *Donatia* and *Phyllachne* only occur in these two regions plus Tasmania. However, the extremely high level of cushion endemism found in Southern New Zealand (63% of species) indicates that it is nevertheless much isolated and that a large part of its cushion species may have originated there. The genus Raoulia is a emblematic example of this local diversification: it bears six species of compact cushions, known as vegetable sheep, that are all endemic to New Zealand.

Limitations of our study and directions for future research

While we are confident that our list of cushion species is almost exhaustive, we recognize that the phylogenetic and biogeographic scales used in this study limit a lot the conclusions that can be drawn. First of all, the number of independent appearings of the cushion life form that we estimated is very conservative, since we had no phylogenetic information inside families. Future studies using phylogenies resolved at the species level in families where the cushion life form is frequent (e.g. Caryophyllaceae, where 19 genera have cushion species) should provide more reliable estimates of the number of appearings of this convergence.

Second, our demonstration that the cushion life form is adapted to cold and dry conditions is rather indirect since we used distribution data for whole families and not individual species. The fact that this adaptation has already been demonstrated in experiments as well as in other phylogenetic studies however makes us confident that this conclusion is correct.

An important subject that we could not tackle in this study due to a lack of phylogenetic resolution is whether cushion generally spurred diversification, as has been shown in the genus Androsace (Roquet et al., 2013). In particular, determining whether cushions have increased speciation rates because they occupy highly fragmented habitats in mountains or if their extreme longevity (e.g. Morris & Doak, 1998) leads to reduced extinction rates, is of primary importance.

Finally, conclusions on the roles of different regions are of course largely speculative, since they heavily rely on taxonomic

treatments and geographic subdivisions that are partly arbitrary. They however provide a first look at the global biogeography of cushion species and suggest directions for future research. Proper biogeographic reconstructions and diversification analyses with phylogenies resolved at the species level would be needed to accurately study the relative contributions of diversification and immigration to richness patterns in these different areas of the globe.

Conclusion

Using a nearly exhaustive catalogue of Angiosperms bearing the cushion life form, we have shown that the cushion life form is a convergent key innovation that has appeared at least 41 times independently in Angiosperms, providing the opportunity to colonize alpine and arctic environments. However, cushions are not randomly distributed in Angiosperms, suggesting that some traits might be prerequisite for this life form to appear. Cushions are present on all major mountain ranges in the World, but we have shown that the main centers of diversity are located in the Himalayas, the Andes, Patagonia and New Zealand. Importantly, while the Himalayas, the Andes, and New Zealand might be cradles of cushion diversity, Patagonia might serve as a hub connecting Austral regions to South America. These results are of primary importance for understanding the origins of alpine floras worldwide.

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SUPPLEMENTARY MATERIALS

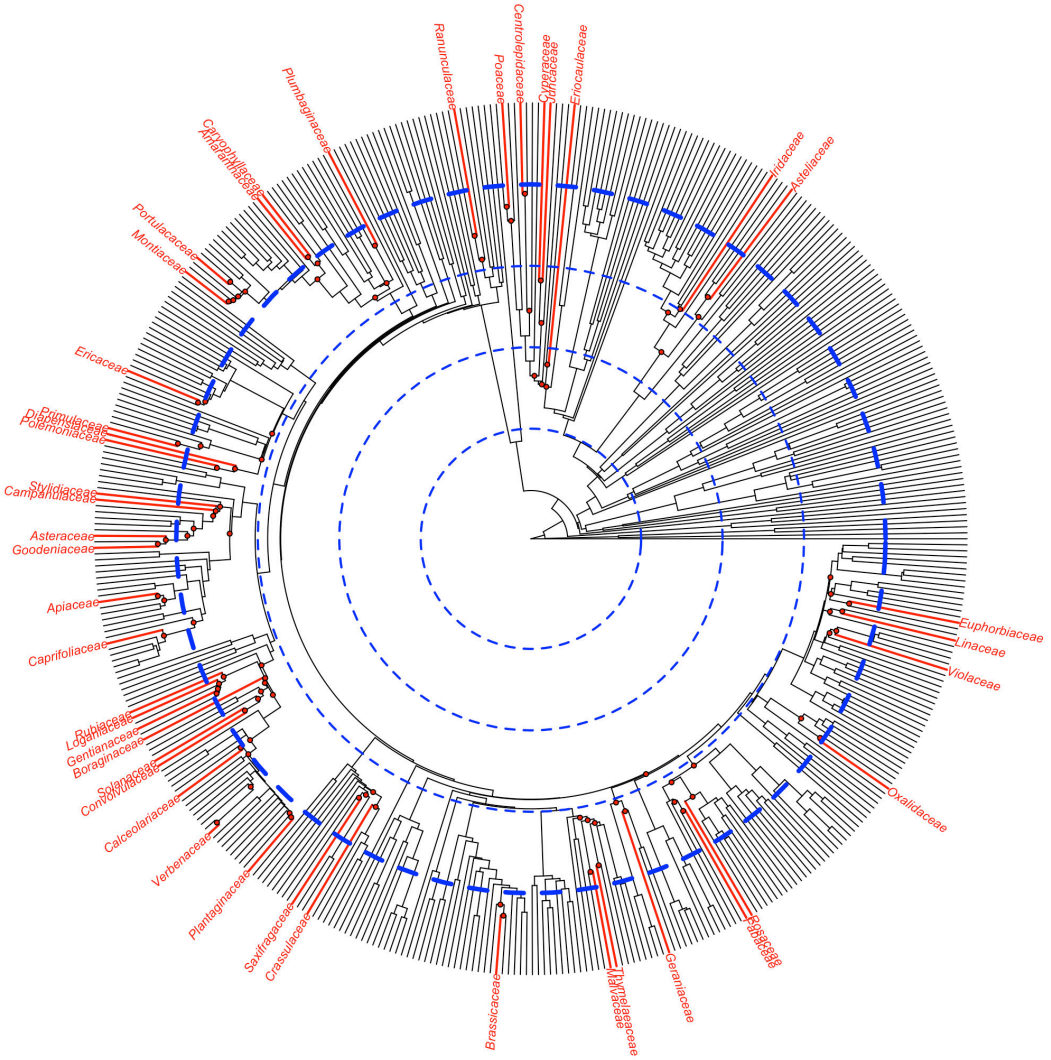

Figure S1: ancestral character estimation of the presence of cushions in Angiosperm families. This plot of the tree of Angiosperm families show families bearing at least one species of cushion in red. Red dots show nodes where the probability that the ancestral species was estimated to be a cushion by parsimony. Most appearings of the cushion life form that are inferred happened before -50 Mya (indicated by thickest blue circle), a situation that is unlikely given that cold biomes did not exist before this period.

DISCUSSION

Dans cette discussion, je commencerai par faire la synthèse des principaux résultats obtenus durant ma thèse, en montrant comment ils contribuent à avancer nos connaissances sur l'évolution des niches climatiques et sur les origines de la flore alpine. Je discuterai ensuite les limitations de mon travail et suggérerai des directions de recherches futures. Enfin, je proposerai quelques perspectives personnelles sur l'apport de la macroévolution à l'étude des changements globaux.

1. SYNTHESE DES RESULTATS OBTENUS

1.1. La distinction entre niche fondamentale et niche réalisée et l'importance de la géographie

Dans le passé, la différence entre l'évolution des niches fondamentales et celle des niches réalisées a été plusieurs fois soulevée du point de vue théorique (Colwell & Rangel 2009, Holt 2009, Peterson 2011) mais jamais, à ma connaissance, cette distinction n'a été utilisée dans des études de macroévolution. La plupart des auteurs ont traité la niche climatique comme un trait fortement déterminé de manière génétique, ce qui a fortement orienté les interprétations des études empiriques vers des causes génétiques directes comme la sélection, la dérive ou la mutation (voir cependant Crisp & Cook 2012).

Dans l'article 1.2 nous avons proposé la première étude démontrant à quel point la distinction entre la niche fondamentale et la niche réalisée est cruciale dans l'étude de l'évolution des niche climatiques. En effet, cette étude de simulation a illustré comment la niche réalisée des espèces peut changer dans le temps sous l'influence de facteurs géographiques neutres comme la migration, la compétition pour l'espace, ou encore les évènements de vicariance ou de spéciation péripatrique, sans qu'aucune caractéristique physiologique de l'espèce n'évolue. Notre travail sur l'influence des facteurs géographiques constitue donc une mise en garde contre des interprétations adaptationistes trop rapides de l'évolution des niches climatiques. Certaines différences de niche climatique entre espèces ne sont probablement en effet dues qu'à des différences de distribution, qui n'ont rien à voir avec les tolérances climatiques des

espèces et sont des sous-produits de processus comme la compétition pour l'espace, la dispersion ou la spéciation. Afin de démontrer clairement que les niches d'un groupe d'espèces ont été sélectionnées, d'autres preuves doivent être apportées, par exemple en étudiant l'influence de traits fonctionnels. C'est ce que nous avons fait pour le genre *Androsace*, nous avons démontré l'influence des différentes formes de vies sur les niches climatiques, mais où toutes les espèces en coussin ont des niches climatiques très similaires (article 3.2).

1.2. Un mode d'évolution général pour les niches climatiques

Le résultat principal de ma thèse, soutenu à la fois par des arguments théoriques (article 1.2) et par des résultats empiriques (article 2, article 3.1), est d'avoir révélé le mode d'évolution général des niches climatiques. En effet, en me basant sur la distinction entre niche fondamentale et niche réalisée, j'ai montré (1) que les niches évoluent généralement sous contrainte, (2) mais aussi de manière ponctuelle. Ces modes d'évolution permettent de proposer (3) un modèle générale d'évolution des niches fondamentales, en (4) distinguant notamment deux grand types de ponctuations.

Contraintes sur la niche climatique des espèces

Dans la majorité des clades étudiés, un modèle d'Ornstein-Uhlenbeck (OU) à plusieurs optima décrivait le mieux l'évolution des niches climatiques. En effet, sur les 125 clades étudiés dans l'article 2, seuls trois se conformaient à un mouvement brownien. Dans le cas d'étude le plus fin que j'ai réalisé, l'étude de l'évolution des niches climatiques du genre *Androsace* (article 3.1), j'ai aussi montré que le meilleur modèle d'évolution des niches climatiques était un modèle OU avec un optimum différent pour chacune des formes de vies. Si ce patron général où la niche évolue suivant un modèle OU est souvent expliqué par de la sélection stabilisante sur la niche climatique des espèces, il peut également être causé par des processus neutres ou des contraintes génétiques. En effet, grâce à l'étude de simulation de l'article 1.2, nous avons montré que de simples processus neutres tels que la migration aléatoire d'individus dans un paysage borné

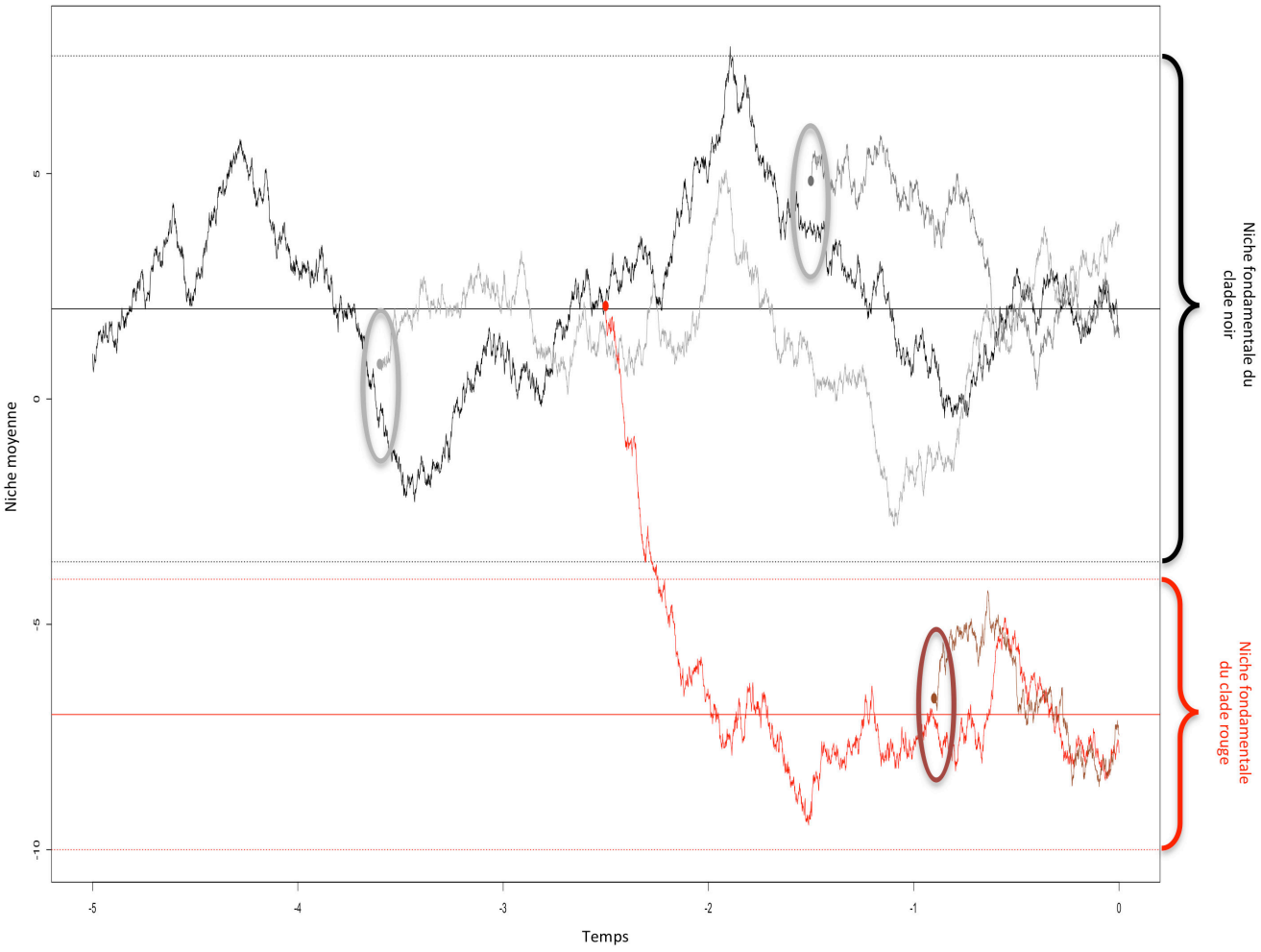

Figure 9. Scénario général de l'évolution des niches climatiques. Les niches réalisées de cinq espèces (valeur moyenne de la niche sur un gradient climatique) sont représentées au cours du temps. L'ancêtre du clade occupe la niche fondamentale noire et sa niche réalisée évolue au sein de l'espace climatique déterminé par cette niche fondamentale. Aux évènements de spéciation, les niches réalisées des espèces filles diffèrent légèrement de celle de l'espèce ancestrale ('petites ponctuations', entourées par les ellipses). Une innovation clef apparaît et permet à l'espèce rouge d'évoluer très rapidement vers une nouvelle niche ('grande ponctuation'). Le clade rouge se diversifie et les niches réalisées y évoluent au sein de cette nouvelle niche fondamentale rouge. Les spéciations y sont toujours accompagnées de ponctuations. Ce scénario est bien sûr une représentation simplifiée de la réalité. Il a été simulé en rajoutant des sauts à la spéciation à un modèle OU à deux optima (noir et rouge).

peuvent conduire au même résultat. Enfin, il est très probable qu'une variabilité génétique limitée pour des traits impliqués dans l'adaptation au climat créerait le même patron d'évolution bornée.

Ces contraintes démontrent que les niches climatiques sont souvent conservées sur des périodes de temps relativement longues (de plusieurs millions d'années), que ce soit de manière active (*i.e.* par la sélection stabilisante sur des traits physiologiques) ou passive (*i.e.* à cause de limitations de dispersion ou d'une variabilité génétique limitée). Ces diverses explications du PNC ont des conséquences différentes sur la capacité des espèces à s'adapter à des climats nouveaux. En effet, si les limitations de dispersion sont la cause principale du PNC, alors il est envisageable que les espèces puissent parfaitement s'adapter à un climat nouveau si celui-ci se présente. Si c'est la sélection qui est le principal agent du PNC, un changement environnemental entraînera une modification de la sélection naturelle (sa direction et/ou sa force), et les espèces pourront éventuellement évoluer en réponse à cette nouvelle pression de sélection. En revanche, si c'est la variabilité génétique qui limite l'évolution des niches climatiques, alors les capacités d'adaptation des espèces seront probablement faibles. La méta-analyse présentée dans le chapitre 2 suggère que la sélection pourrait être un agent important du PNC, alors que les limites de dispersion et la variabilité génétique auraient un rôle moindre. Toutefois, les proxys utilisés pour caractériser ces trois causes potentielles du PNC étaient indirects et des études plus fines où la variabilité génétique des espèces et la sélection seraient directement mesurées sont nécessaires pour trancher définitivement cette question. Les multiples exemples d'invasion biologiques devraient permettre de mieux comprendre les conséquences d'une levée des limitations de dispersion sur la niche climatique des espèces (voir Holt et al. 2005, Petitpierre et al. 2011, Gallien et al. 2012).

Evolution ponctuelle des niches climatiques

Les résultats obtenus durant ma thèse montrent également que l'évolution des niches climatiques se fait souvent par 'à-coups' brusques. Deux types d'indices soutiennent ce résultat. Tout d'abord, les indices de ponctualisme que j'ai utilisé (ψ d'Ingram dans le chapitre 2, κ de Pagel dans le chapitre 3) montrent qu'en général, une large proportion de la variance des niches climatiques dans un clade peut être attribuée à des changements liés aux évènements de spéciation plutôt qu'à une évolution graduelle durant l'anagénèse. Les comparaisons de modèles ont également montré que le modèle le plus probable pour l'évolution des niches climatiques est très souvent un modèle

d'Ornstein-Uhlenbeck avec plusieurs optima (voir chapitres 2 & 3), où les niches des espèces restent contraintes pendant de longues périodes (stase) mais où des transitions rapides entre ces différents optima s'effectuent de manière assez fréquente (ponctuation). Notons que ces deux mesures ne sont pas équivalentes et révèlent des ponctuations à différents niveaux. En effet, une évolution largement ponctuelle a été détectée dans des clades où un modèle OU à un seul optimum est le scénario privilégié (par exemple le genre *Capsicum* et la famille des Musophagidae, voir article 2), ce qui montre que ce ne sont pas uniquement les transitions entre différents optima d'un modèle OU qui conduisent à mesurer du ponctualisme. Mon travail théorique (article 1.2) a également montré qu'une évolution ponctuelle pouvait se produire bien que toutes les espèces restent contraintes par le même régime de sélection. Nous avons donc mis en évidence que des ponctuations se manifestent à deux niveaux différents dans l'évolution des niches climatiques : d'abord lors des phases où la niche est contrainte sous la forme de 'petites ponctuations' autour d'un optimum de niche donné, lors des évènements de spéciation ; également par de 'grandes ponctuations' qui permettent de passer d'un optimum de niche à un autre, mais sont plus rares (en moyenne un évènement de spéciation sur huit, voir article 2).

Des études théoriques ont montré que des ponctuations peuvent se produire lorsque des populations d'une espèce parviennent à passer d'un pic de fitness à un autre en franchissant une vallée du paysage adaptatif de l'espèce. Ceci peut arriver grâce à l'apparition d'une ou plusieurs mutations qui confèrent une adaptation à un nouvel environnement (Holt et al. 2003), si les deux pics de fitness se rapprochent au cours du temps (Kirkpatrick 1982), ou encore suite à une augmentation de la variabilité génétique permettant de franchir la vallée de fitness (Kirkpatrick 1982). Mon travail (article 1.2) a également mis en évidence la possibilité de ponctuations sans qu'aucune modification génétique ne produise, le changement des niches climatiques réalisées pouvait être simplement la conséquence de la séparation géographique de deux espèces sœurs à la suite d'une spéciation.

Un modèle général pour l'évolution des niches fondamentales et des niches réalisées

Le modèle général d'évolution des niches climatiques que ma thèse a révélé est donc

constitué de deux grands types d'évènements : (i) des phases de stase : périodes relativement longues durant lesquelles les niches sont soumises à des contraintes et évoluent peu ; (ii) des phases de transition : brèves périodes suivant certains évènements de spéciation durant lesquelles les niches climatiques évoluent rapidement. J'interprète ce scénario général de la manière suivante (voir Figure 9):

(i) les phases de stase sont dues soit à de véritables contraintes génétiques sur la niche fondamentale d'un groupe d'espèces (sélection stabilisante, manque de variabilité, etc.) soit à des barrières géographiques très peu perméables qui contraignent le groupe d'espèces à n'utiliser qu'une partie de leur niche fondamentale. Soulignons que dans le second cas, il est fort probable que si ces barrières perdurent pendant très longtemps, la niche fondamentale des espèces s'ajuste peu à peu aux conditions présentes dans leur aire de distribution en purgeant les adaptations 'inutiles' à des climats qui n'ont pas été expérimentés depuis longtemps. Au cours de ces phases de stase, les niches fondamentales de toutes les espèces d'un groupe restent assez similaires et évoluent peu. Au contraire, leurs niches réalisées peuvent évoluer sous l'influence de facteurs indirects (les interactions biotiques et la migration), et effectuent de petites ponctuations lors des évènements de spéciation (Figure 9), probablement dues à la séparation géographique liée à la spéciation (voir chapitre 1).

(ii) les phases de transitions qui permettent de passer d'un régime de contrainte à un autre (Figure 9) représentent pour moi des changements de niche fondamentale. Les causes possibles de ces changements de niche fondamentale sont variées : apparition d'un caractère morphologique permettant d'occuper de nouveaux climats (comme la forme de vie en coussin, voir chapitres 3 & 4), innovation physiologique (comme la photosynthèse en C4, voir Sage 2004, Edwards et al. 2010), modification comportementale (apparition de la migration, ou de l'hibernation), etc. Ce sont par définition toutes des innovations clefs (*sensu* Miller 1949), puisqu'elles permettent aux espèces de coloniser de nouveaux environnements. Elles permettent une évolution très rapide des niches climatiques, et peuvent donc induire de 'grandes ponctuations' (Figure 9).

Deux types de ponctuations différentes

Les deux types de ponctuations présentées plus haut sont de nature différente. Les petites ponctuations qui ont lieu lors des phases de stase de la niche fondamentale ont été clairement liées aux évènements de spéciation. En effet, les indices qui les ont révélées testent la vraisemblance d'un modèle d'équilibre ponctué contre celle d'un modèle purement gradualiste (articles 2.1 et 3.1) et le modèle de simulation du chapitre 1.3. en a montré un mécanisme possible : la géographie de la spéciation. Dans ce cas, il paraît probable que ce soit la niche réalisée des espèces qui évolue de manière ponctuée et que la spéciation n'ait aucun rôle actif dans cette explication. Cette situation rejoint l'explication de l'équilibre ponctué proposée par Futuyma (1987) et reprise par Gould dans ses derniers écrits (2002) : dans l'équilibre ponctué, la spéciation n'a pour seul rôle que d'enregistrer les modifications qui se produisent continuellement au niveau des populations. En effet, la microévolution a montré que des changements évolutifs se produisent constamment au sein des populations (adaptation locale, dérive), même sur des temps très courts (Reznick et al. 1997, Losos et al. 1997, Phillips et al. 2006). Dans la majorité des cas, ces modifications sont gommées par les flux de gènes entre populations et ces changements évolutifs sont donc éphémères du point de vue macroévolutif. En revanche quand la spéciation se produit, différentes populations se retrouvent isolées et ces modifications sont moins facilement effacées (Futuyma 1987, Gould 2002).

Dans le cas des grandes transitions entre différent optimum de niche, on s'attend à ce que ce soit plutôt la niche fondamentale qui effectue des ponctuations (voir l'exemple détaillé d'*Androsace*, chapitre 3). Le lien avec les évènements de spéciation est moins clairement établi dans ce cas: les modèles utilisés (OU avec plusieurs optima) font en effet cette hypothèse, mais elle n'est pas testée contre un scénario alternatif où ces changements d'optimum se produiraient pendant l'anagénèse. Il est en particulier possible que la spéciation initie une phase d'évolution importante de la niche fondamentale, mais que cette évolution ne soit pas à proprement parler ponctuelle (voir Holt et al. 2003, Ricklefs 2004, Pennell et al. 2013 pour une discussion approfondie de ce point). Il est également probable que la causalité soit inversée dans ce cas et que de tels changements de niche conduisent à l'isolation géographique de différentes populations

et entraînent la spéciation. Les explications théoriques de l'évolution ponctuelle fournies par la microévolution semblent mieux s'appliquer dans ce cas, où de nombreuses modifications génétiques sont probablement requises. Il est ainsi probable que ces innovations clefs soient causées par des changements du paysage adaptatif ou apportées par de nouvelles mutations (Kirkpatrick 1982, Holt et al. 2003). Ces grandes transitions n'ayant pas forcément lieu lors de la spéciation et ne se produisant que de manière occasionnelle, elles ne se conforment pas exactement au modèle de l'équilibre ponctué (Gould & Eldrege 1977). Ces évènements s'apparentent donc plutôt à des sauts entre différents pics d'un paysage adaptatif macroévolutif (Simpson 1953). Ces transitions entre pics sont néanmoins rapides du point de vue de la macroévolution, et sont relativement fréquentes.

1.3. Premiers éléments de réponse sur l'origine de la flore alpine

Ma thèse a également permis de fournir des éléments de réponse importants sur l'origine de la flore des Alpes en particulier et des flores des régions alpines et arctiques en général. Pour cela, je me suis concentré sur les espèces d'Angiospermes en coussin. Ce travail était nécessaire car l'histoire de la flore des environnements alpins a été jusqu'ici très peu étudiée par rapport à celle d'autres écosystèmes comme les régions Méditerranéennes (Valente & Vargas 2013) ou les systèmes insulaires (Gillespie et al. 2012).

Un résultat important que nous avons obtenu est que ces flores des différentes régions alpines sont formées d'éléments disparates, recrutés dans les flores des régions avoisinantes. En effet, notre travail sur *Androsace* a montré que les espèces en coussin occupant des habitats extrêmes dans les Alpes (les membres de la section *Aretia*) ont évolué sur place à partir d'ancêtres qui n'étaient pas des coussins, mais des plantes à durée de vie plus courte, probablement adaptées aux steppes froides. D'autres espèces en coussin du monde sont des exemples encore plus frappants : *Deuterocohnia brevifolia* appartient en effet à la famille des Bromeliacées, qui est typique des régions tropicales humides et contient une majorité d'épiphytes. Le nombre élevé de genres différents qui possèdent des espèces en coussin compactes (156 genres chez les Angiospermes, cf.

chapitre 4), y compris au sein d'une même région (40 genres en Patagonie argentine, 31 au Pérou, 23 dans l'île Sud de la Nouvelle Zélande) confirme que ces espèces des milieux arctiques et alpins ont été recrutées à partir de nombreux taxons différents. Ce résultat corrobore ceux obtenus sur la flore arctique, où la majorité des espèces (et non pas seulement les coussins) proviennent d'espèces non-arctiques (Hoffmann & Roser 2009).

Ces très nombreuses convergences vers la forme de vie en coussin dans des lignées de plantes très diverses suggèrent que les pressions de sélection pour une adaptation au froid ont donc dû être extrêmement fortes au moment de l'apparition des environnements alpins sur Terre. Cependant, de nombreuses lignées ont réussi à répondre à ces pressions de sélection, ce qui montre que l'adaptation à des climats froids est assez facile ou en tout cas qu'elle a été souvent possible. Une étude récente sur les tolérances physiologiques de nombreuses espèces de plantes, d'insectes et de vertébrés a confirmé que l'extrême froid de la niche des espèces est beaucoup plus labile que leur extrême chaud (Araujo et al. 2013). En étudiant le cas du genre *Androsace*, nous avons mis en évidence que l'adaptation aux climats alpins a été relativement rapide. En effet, la forme de vie en coussin est apparue dans les Alpes quelques millions d'années seulement après que ce massif ne soit colonisé (Boucher et al. 2012, Roquet et al. 2013).

Le recrutement d'espèces depuis un pool local de plantes non arctico-alpines n'est cependant pas une règle absolue et nous avons montré que malgré leur isolation les différentes régions froides du globe ont également échangé de nombreuses espèces. Ainsi par exemple les espèces du genre *Douglasia* qui sont distribuées en Amérique du Nord (Alaska et Montagnes Rocheuses principalement) sont issues d'une espèce d'*Androsace* en coussin qui vivait en Europe de l'Ouest (Roquet et al. 2013). Les nombreuses espèces en coussin du genre *Draba*, que l'on retrouve dans quasiment toutes les régions froides du monde, suggèrent également que de nombreux échanges floristiques entre ces régions ont eu lieu. En étudiant les coussins dans l'ensemble des Angiospermes, nous avons même suggéré que certaines régions ont joué un rôle important de plaque tournante biogéographique, permettant la connexion entre différentes régions froides du globe et les échanges floristiques. La Patagonie en est l'exemple parfait puisqu'elle a servi de connexion entre les régions subantarctiques (Nouvelle Zélande, Tasmanie et îles subantarctiques) et les Andes. De la même façon, les montagnes de Turquie ou d'Iran ont probablement permis le passage de nombreuses

espèces alpines entre l'Himalaya et les Alpes.

Finalement, d'autres régions ont au contraire plutôt été des berceaux de diversité pour les espèces arctico-alpines. L'article 4.2 suggère que l'Himalaya, les Andes, la Nouvelle Zélande et dans une moindre mesure les Alpes et les Pyrénées sont les principaux centres de diversification des espèces en coussin. En comparaison, peu d'espèces seraient apparues dans les Montagnes Rocheuses ou dans la zone Holarctique. La richesse floristique de ces régions alpines, même si elle est moindre que celle des Tropiques, est relativement élevée (Orme et al. 2005, McCain & Colwell 2011) pour des environnements si jeunes et si peu productifs. Nous avons montré que dans le genre *Androsace* les espèces en coussin ont diversifié plus rapidement que leurs congénères occupant des milieux plus cléments. L'explication la plus plausible pour cette différence semble être liée à la fragmentation des habitats alpins. En effet, dans des systèmes en archipel comme c'est souvent le cas des environnements alpins, les occasions de spéciation allopatrique sont assez fréquentes, conduisant à la création de nombreuses espèces qui sont largement semblables écologiquement. Le nombre d'espèces en coussin bien plus faible rencontré dans les régions arctiques va dans le sens de cette explication, car les zones arctiques du globe, même si elles occupent une surface bien plus importante que les régions alpines, sont beaucoup moins fragmentées. Les vitesses de diversification relativement élevées des flores alpines du globe ne semblent donc pas être dues à un effet direct de la température (au contraire la spéciation semble être favorisée par les températures chaudes, qui causent plus de mutations, Wright et al. 2006, Allen et al. 2006), mais plutôt à la fragmentation des habitats alpins.

2. LIMITATIONS DE MON TRAVAIL ET DIRECTIONS FUTURES

2.1. Limitations et développements méthodologiques pour l'étude de l'évolution des niches

Si j'ai essayé de clarifier la méthodologie utilisée pour étudier l'évolution des niches climatiques dans le premier chapitre de ma thèse, cette partie a aussi mis en évidence les limites de la méthodologie actuelle. Développer des algorithmes rapides pour estimer des modèles complexes me semble être une des grandes priorités méthodologiques. Si de telles avancées on été réalisée pour les modèles simples (Freckleton 2012), il reste encore à les implémenter pour des modèles flexibles comme des modèles OU à plusieurs régimes de sélection où tous les paramètres peuvent varier (intensité de la sélection, vitesse de la dérive) au sein de la phylogénie. Le nombre croissant de mégaphylogénies contenant des centaines voire des milliers de taxons stimulera sans doute ces développements. D'autres avancées sont également souhaitables, en particulier de développement de modèles incluant l'influence des interactions entre espèces sur l'évolution des traits. Les analyses de diversification ont récemment commencé à prendre en compte ces interactions et ont montré qu'une part importante des phylogénies montre des traces de compétition entre espèces pour la diversification (Morlon et al. 2010). Pour l'instant, tous les modèles d'évolution des traits font l'hypothèse que les espèces évoluent de manière indépendante, ce qui très peu réaliste (voir les simulations du chapitre 1.3 ou Mahler et al. 2010). J'ai commencé à développer un modèle de simulation incluant de la compétition entre espèces en me basant sur des modèles de déplacement de caractère existant en microévolution (*e.g.* Doebeli 1996), mais inférer les paramètres de ce modèle sur des données empiriques s'est avéré très difficile. L'essor rapide des méthodes ABC en écologie et en évolution (Csilléry et al. 2010, Jabot et al. 2013) permettra peut être de relever ce défi. Enfin, les chapitres 3 et 4 de ma thèse ont souligné les conséquences de l'évolution des niches climatique sur la biogéographie et la diversification. Certaines méthodes permettent déjà d'étudier ensemble évolution des traits et diversification (Maddison et al. 2007) ou biogéographie et diversification (Goldberg et al. 2011), mais elles sont pour l'instant

limitées à des cas particuliers (taux de diversification constants dans le temps, traits qui évoluent de manière brownienne). Le développement de méthodes permettant d'étudier évolution des traits, biogéographie et diversification de manière simultanée est très souhaitable.

Cependant, ces modèles complexes auront un nombre de paramètres élevé et il n'est pas évident que tous ces paramètres puissent être estimés correctement avec le peu de données fournies : un trait par espèce et une phylogénie. Des approches de simulations permettant d'estimer la puissance des méthodes comparatives commencent à se développer et elles ont déjà révélé que dans certains cas, il était extrêmement difficile de choisir entre différents modèles, en particulier sur des petites phylogénies (Boettiger et al. 2012). Leur utilisation se généralisera très probablement dans les années à venir. L'incorporation de données fossiles ou d'informations sur les paléo-environnements permettra aussi d'apporter plus d'informations à ces analyses statistiques, en renseignant sur les valeurs possibles des caractéristiques des espèces ancêtres (Hutter et al. 2013) et en excluant donc certains scénarios improbables.

Une avancée méthodologique qui me paraît cruciale mais sera plus difficile à réaliser consistera à incorporer la variabilité intra-spécifique dans les analyses comparatives. En effet, une quantité d'information énorme est perdue quand chaque espèce est résumée par son trait moyen. Mon travail a montré en particulier que la niche moyenne d'une espèce est une caractéristique qui résume assez mal l'évolution des niches climatiques (article 1.2). Des études de terrain sur les plantes alpines auxquelles j'ai participé ou que j'ai dirigées ont non en effet mis en évidence que les traits fonctionnels varient fortement au sein des espèces et même des populations (Albert et al. 2010, Boucher et al. 2013). Des approches statistiques ont déjà été proposées pour modéliser la variabilité intra-spécifique en macroévolution, mais elles traitent la variabilité intra-spécifique comme une erreur de mesure (une source de variance supplémentaire dans un modèle mixte, voir Felsenstein 2008). Modéliser de manière plus explicite l'évolution des traits au sein des espèces demandera d'être capable de représenter l'histoire des individus au sein d'une même espèce, en utilisant par exemple le processus du coalescent (Kingmann 1982). Intégrer phylogénie entre espèces et relations de parenté entre individus dans chaque espèce demandera de l'imagination pour créer de nouveaux modes de représentation mais ouvrira la voie à une meilleure intégration de la macro et

de la micro-évolution.

Tous ces développements méthodologiques nécessiteront de disposer de phylogénies datées. La phylogénie d'un clade est toujours supposée parfaitement connue en analyse comparative (Harvey & Pagel 1991), et toutes les inférences que nous tirons sur l'évolution des traits reposent sur sa qualité. Les méthodes utilisées pour construire des phylogénies (reconstruction, calibration, etc.) connaissent un développement rapide grâce aux avancées en bioinformatique, mais estimer la phylogénie d'un groupe et la dater avec précision restent compliqués (Wertheim et al. 2011, Sanderson et al. 2011, Christin et al. 2012). En attendant que les méthodes de reconstruction phylogénétique ne se perfectionnent encore, il paraît plus raisonnable pour les analyses comparatives de ne pas se fier aveuglement à une phylogénie donnée. Utiliser de nombreux arbres (comme nous l'avons fait chez *Androsace*) ou même éventuellement tester la robustesse des résultats à des 'perturbations' (modification des longueurs de branches, changements de topologie, etc.) de la phylogénie d'un clade permettent d'intégrer l'incertitude phylogénétique.

2.2. Etudier l'évolution des tolérances physiologiques des espèces

La limitation principale de ma thèse a été de n'avoir utilisé que des données de distribution pour caractériser les niches climatiques des espèces, ce qui nous a empêché de mesurer leurs niches fondamentales. Mesurer les tolérances physiologiques d'un grand nombre d'espèces dans des conditions expérimentales permettra de mieux comprendre les mécanismes responsables de l'évolution des niches climatiques (voir Kellermann et al. 2012, Araujo et al. 2013). Ceci permettrait en particulier de distinguer évolution de la niche fondamentale et évolution de la niche réalisée, une étape nécessaire pour confirmer le scénario global d'évolution des niches climatiques que j'ai suggéré plus haut.

A défaut de mesures physiologiques fines, qui sont difficiles à obtenir sur un grand nombre d'espèces, l'étude de certains traits fonctionnels liés à l'adaptation au climat (surface spécifique foliaire ou contenu en matière sèche des feuilles chez les plantes) pourrait être une alternative plus facile à envisager. Il serait intéressant de ne pas

étudier ces traits fonctionnels séparément mais plutôt des syndromes de traits. En effet, des compromis de traits universels ont été révélés, comme le 'Leaf Economics Spectrum' qui décrit les corrélations entre différents traits fonctionnels foliaires (Wright et al. 2004), mais l'évolution de ces syndromes reste inconnue. Pour comprendre comment ces syndromes se sont mis en place et ont évolué au cours de l'histoire des plantes terrestres de larges jeux de données de traits fonctionnels, mais surtout des avancées méthodologiques seront nécessaires pour modéliser l'évolution corrélée de nombreux traits.

Les travaux que j'ai réalisé sur *Polygonum viviparum* L. durant ma thèse ont permis de révéler des situations différentes en limites chaudes et froides de la distribution de cette espèce alpine distribuée dans tout l'Hémisphère Nord: en effet, alors que les individus des environnements les plus chauds ont des traits fonctionnels très variables et peu corrélés, ceux des environnements les plus froids ont tous des traits similaires et soumis à de forts compromis (Boucher et al. 2013). Ce travail va être complété par une étude moléculaire et les résultats d'une expérience en jardin commun qui permettront de déterminer la part de cette variabilité phénotypique qui est d'origine génétique. Ces études devraient permettre de mieux comprendre les processus responsables des limites de distribution des espèces végétales alpines.

2.3. Examiner en détail l'évolution ponctuée des niches climatiques

Les analyses menées durant ma thèse pointent vers une évolution ponctuée des niches climatiques des espèces. Cependant, ce résultat provient d'analyses statistiques sur des clades de plusieurs dizaines d'espèces, mais les détails de ce processus restent à examiner finement. En particulier, le rôle de la spéciation dans ce processus reste à déterminer : la spéciation joue-t-elle un rôle neutre, limité à enregistrer des changements qui ont eu lieu dans des populations lorsqu'elles se retrouvent isolées reproductivement (Futuyma 1987) ou au contraire est-ce la divergence des tolérances climatiques de différentes population qui engendre leur isolation reproductive ? Les avancées techniques de la génomique ces dernières années et leur application aux questions liées à la spéciation (Nosil 2012) devraient permettre de pouvoir déterminer

qui des loci d'incompatibilité ou des loci d'adaptation au climat divergent souvent en premier et donc de révéler la direction de causalité la plus probable. Mener de telles études à des échelles fines, incluant différentes populations d'un groupe de quelques espèces proches devrait aussi révéler si le changement de niche climatique se produit réellement durant le processus de spéciation ou si la spéciation initie une divergence de niche qui se poursuit longtemps après qu'elle soit complète (Ricklefs 2004, Pennell et al. 2013). Au passage, ces approches génomiques montreront clairement si ces groupes d'espèces divergent réellement à des loci d'adaptation au climat, ou si au contraire ce ne sont que leurs niches réalisées qui diffèrent.

2.4. Questions ouvertes sur la diversité des espèces végétales alpines

Notre travail sur les espèces d'Angiospermes en coussin a révélé certaines grandes causes de la diversité des flores alpines : un recrutement d'espèces depuis des lignées variées présentes localement suivi d'une diversification *in situ*, mais aussi des échanges d'espèces entre différentes régions. Cependant, de nombreuses questions n'ont pu être abordées à une échelle aussi large et restent donc ouvertes.

Tout d'abord, le scénario général de l'évolution des plantes alpines que nous avons proposé à partir de l'étude d'*Androsace* devrait être vérifié sur d'autres groupes. Pour cela, il faudra réussir à obtenir de nombreuses phylogénies de groupes de plantes alpines et non alpines et les dater. Ceci permettra de vérifier si l'adaptation aux habitats alpins s'est fait au fur et à mesure des orogénèses, ou si au contraire des temps d'attente longs ont été nécessaires, comme cela a été le cas pour la colonisation du désert d'Atacama par différents groupes de plantes et de lézards (Guerrero et al. 2013). Bien sûr, des données fines sur l'évolution des reliefs et des climats des principales chaînes de montagnes du monde seront nécessaires pour réaliser de telles études.

L'exemple d'*Androsace* a également montré que les taux de diversification des espèces en coussin on été plus élevés que ceux des autres espèces du genre (Roquet et al. 2013). D'autres groupes de plantes alpines ont également diversifié très rapidement (espèces alpines du genre *Lupinus*, Hughes & Eastwood 2006). Ces exemples suggèrent que les espèces végétales alpines ont rencontré une forte opportunité écologique, c'est-à-dire

des environnements peu exploités par d'autres espèces (Glor 2010, Yoder et al. 2010), lorsqu'elles ont colonisé les environnements alpins lors des orogénèses. Cette opportunité écologique l'aurait même emporté sur les contraintes métaboliques imposées par le froid. Ce scénario devrait être vérifié sur d'autres groupes afin de l'établir clairement et de tester sa généralité. Enfin, étudier la diversification de différents groupes qui ont colonisé les environnements alpins les uns après les autres permettra de savoir si les premiers arrivants ont rencontré plus d'opportunité que ceux qui les ont suivis (*i.e.* si les groupes suivants ont diversifié moins vite), comme cela a été établi dans l'île Sud de la Nouvelle Zélande (Lee et al. 2012).

Concernant la diversification, le rôle des falaises d'altitude comme sources de diversité mériterait aussi d'être examiné. En effet, ces habitats sont probablement restés relativement stables lors des changements environnementaux passés : les grandes falaises n'ont pas été entièrement englacées et ont constitué des refuges pour la végétation (les nunataks, Schneeweiss & Schoenswetter 2011). De plus, la compétition entre espèces ainsi que l'herbivorie y sont moins importantes que dans les prairies alpines avoisinantes. Ces deux phénomènes pourraient conduire à des taux d'extinction plus faibles chez les plantes qui les occupent, faisant des falaises des 'musées de diversité' (à l'échelle des environnements alpins bien sûr).

Si l'étude de phylogénie permet de révéler certaines causes principales de la diversification, les causes proximales de la spéciation dans les environnements alpins sont encore mal connues. La diversité fonctionnelle est souvent plus faible dans ces environnements et de nombreuses convergences fonctionnelles y sont observées, que ce soit entre espèces (voir chapitre 4), ou même au niveau intraspécifique (Boucher et al. 2013). Il est donc peu probable que la spéciation chez les plantes alpines soit principalement causée par des divergences fonctionnelles (comme l'exige la spéciation écologique, Nosil 2012) et l'isolement géographique y joue sûrement un rôle important. Il est donc nécessaire d'étudier finement le processus de spéciation entre espèces alpines afin de déterminer l'importance relative de ces différents facteurs. Chez *Androsace*, deux espèces sœurs distribuées dans les Alpes, *A. helvetica* et *A. pubescens*, paraissent être le modèle d'étude idéal. Ces deux espèces occupent toutes les deux le même habitat : des fissures de rocher dans des falaises de haute montagne, situées entre 2500 et 4000m et présentent des différences morphologiques plutôt minimes. Elles sont

même parfois observées en sympatrie, dans la même fissure (observation personnelle sur la crête allant du Col du Galibier au Pic Blanc du Galibier) et des hybrides naturels ont été décrits (*A.* x *hybrida* A. Kern). Les deux espèces diffèrent cependant par leurs préférences pour des substrats différents: en effet, *A. helvetica* est plutôt calcicole alors qu'*A. pubescens* est silicicole. L'étude de populations de ces deux espèces ainsi que de leurs hybrides pourrait permettre de déterminer si l'adaptation à des substrats différents est responsable de leur spéciation, et si l'isolation géographique de différentes populations dans le passé a joué un rôle.

Mis ensemble, tous ces aspects de l'évolution de la flore alpine aideront à mieux comprendre les origines de la diversité des milieux alpins. Pour l'instant, étant donné les différents résultats obtenus sur les plantes en coussin durant ma thèse, je pencherais pour un modèle de 'sortie des vallées', inspiré du modèle 'Out of the Tropics' de Jablonski et al. (2006, 2013). En effet, il semble que de nombreuses lignées aient été capables de coloniser les environnements alpins depuis les plaines avoisinantes, même si ces évènements restent rares par rapport au nombre de familles d'Angiospermes. De plus, certains exemples montrent que les taux de diversification peuvent être relativement élevés dans les environnements alpins. La flore alpine serait donc moins riche que la flore des régions tropicales ou même tempérées non pas parce que l'adaptation aux climats alpins serait extrêmement difficile (Latham & Ricklefs 1993, Wiens & Donoghue 2004) ou parce que les taux de diversification nets seraient systématiquement plus faibles dans les habitats alpins (Stebbins 1974), mais simplement parce que ces environnements sont plus jeunes et ont eu moins de temps pour accumuler des espèces. Les grandes lignes de ce scénario restent bien sûr à vérifier en étudiant de nombreux clades comprenant des espèces alpines. De plus, certains détails restent à éclaircir comme dissocier les taux de spéciation des taux d'extinction ou déterminer si les capacités de charge des milieux alpins (*i.e.* le nombre d'individus et d'espèces qu'ils peuvent supporter) diffèrent de celles des milieux tropicaux ou tempérés.

3. PERSPECTIVES PERSONNELLES SUR LA MACROEVOLUTION ET LES CHANGEMENTS GLOBAUX

Lorsque j'ai entamé ma thèse, j'espérais que mon travail sur l'évolution des niches climatiques permettrait de fournir des réponses à la question de la survie des espèces face au réchauffement climatique. Mes premiers travaux sur le genre *Androsace* montraient en effet que leurs niches climatiques avaient beaucoup évolué et fournissaient un message optimiste. Au cours de ma thèse, j'ai réalisé qu'il est impossible de répondre à cette question de société avec les méthodes macroévolutives. En effet, les phylogénies ne permettent pas de comprendre les processus qui agissent à des échelles temporelles inférieures à celle de la branche d'un arbre phylogénétique (même en utilisant des modèles sur-paramétrés), soit des intervalles de temps de l'ordre de 100,000 ans au million d'années chez les plantes ou les vertébrés. Il est donc impossible de prédire à partir de ces connaissances ce qui se passera dans les 100 prochaines années.

Aujourd'hui, de nombreux articles tentent de répondre à la question de l'avenir des espèces face au changement climatique en utilisant des approches macroévolutives, et se heurtent à l'incohérence des échelles de temps mises en jeu. En particulier, les vitesses d'évolution des niches climatiques dans le passé sont parfois comparées à celles qui seraient requises pour faire face au changement climatique (voir par exemple Quintero & Wiens 2013). Ces études concluent toujours que les niches ont évolué bien plus lentement dans le passé que ce qui serait requis pour faire face au changement climatique actuel ; ceci n'a rien d'étonnant si l'on réalise que ces vitesses d'évolution sont moyennées au moins sur des centaines de milliers d'années (sur des branches de l'arbre phylogénétique).

La communauté devrait plutôt admettre que certaines questions ne pourront pas être abordées en étudiant des phylogénies (Losos 2011). Par contre, la macroévolution est la seule à pouvoir aborder certaines autres questions, et notamment celles liées à l'histoire lointaine de la vie sur Terre. Même si la pauvreté relative du registre fossile ou le peu d'informations sur le passé des espèces que contient une phylogénie entraînent de

nombreuses incertitudes et doivent inciter à la prudence dans les interprétations, aucune autre branche de la biologie ne peut aborder le passé lointain.

La macroévolution a donc bien sûr son mot à dire sur les changements globaux et la crise actuelle d'extinction de la biodiversité. Décrire la biodiversité et comprendre ses origines, expliquer les extinctions de masse du passé et les radiations impressionnantes qui ont suivi, souligner le caractère contingent de l'évolution, voici des tâches bien 'utiles' pour la société et fondamentales pour la biologie, que seule la macroévolution peut entreprendre. Si ces résultats ne permettront probablement pas de faire des prédictions sur l'avenir de la biodiversité, ils mettront sans doute en évidence l'importance de certains facteurs pour la survie des espèces face aux changements environnementaux, comme la possibilité de migrer vers des habitats favorables (Donoghue 2008), une structuration en méta-populations faible ou intermédiaire (Jablonski 1986, Gaggiotti & Hanski 2004) ou encore une forte variabilité intra-spécifique (Lloyd & Gould 1993). Beaucoup de travail reste à faire pour décrire l'impact des changements environnementaux du passé sur la biodiversité et comprendre les processus qui ont été mis en jeu lors de ces épisodes.

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ANNEXE :

ARCHITECTURE DE LA VARIABILITE FONCTIONNELLE DANS DES POPULATIONS NATURELLES DE *POLYGONUM VIVIPARUM* L.

Functional Ecology

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Unravelling the architecture of functional variability in wild populations of *Polygonum viviparum* L.

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Summary

1. Functional variability (FV) of populations can be decomposed into three main features: the individual variability of multiple traits, the strength of correlations between those traits and the main direction of these correlations, the latter two being known as 'phenotypic integration'. Evolutionary biology has long recognized that FV in natural populations is key to determining potential evolutionary responses, but this topic has been little studied in functional ecology.

2. Here, we focus on the arctico-alpine perennial plant species *Polygonum viviparum* L.. We used a comprehensive sampling of seven functional traits in 29 wild populations covering the whole environmental niche of the species. The niche of the species was captured by a temperature gradient, which separated alpine stressful habitats from species-rich, competitive subalpine ones. We sought to assess the relative roles of abiotic stress and biotic interactions in shaping different aspects of functional variation within and among populations, that is, the multi-trait variability, the strength of correlations between traits and the main directions of functional trade-offs.

3. Populations with the highest extent of functional variability were found in the warm end of the gradient, whereas populations exhibiting the strongest degree of phenotypic integration were located in sites with intermediate temperatures. This could reveal both the importance of environmental filtering and population demography in structuring FV. Interestingly, we found that the main axes of multivariate functional variation were radically different within and across population.

4. Although the proximate causes of FV structure remain uncertain, our study presents a robust methodology for the quantitative study of functional variability in connection with species' niches. It also opens up new perspectives for the conceptual merging of intraspecific functional patterns with community ecology.

Key-words: alpine plants, ecological niche, functional traits, intraspecific variation, lines of least resistance, phenotypic integration, variance-covariance matrix

Introduction

Intraspecific phenotypic variability has recently emerged as an important topic in the field of plant community ecology (Violle *et al.* 2012). Several studies have shown that, contrary to previous expectations, plant functional traits that vary between species across environmental gradients and are related to community assembly could also be highly variable within species and even within populations (Shipley & Almeida-Cortez 2003; Albert *et al.* 2010b). Accounting for this variability has proven to be crucial in answering various questions in plant ecology (see Jung *et al.* 2010 for community assembly; de Bello *et al.* 2011 for diversity measures; De Frenne *et al.* 2011 for functional strategies). To date, the study of intraspecific phenotypic variability in community ecology has remained mainly univariate (i.e. traits were studied separately, Violle *et al.* 2012 but see Reich *et al.* 2003; Albert *et al.* 2010a), although it is the entire trait syndrome that influences individual's fitness and can be linked with species'

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environmental niches (Reich *et al*. 2003; Wilson & Nussey 2010). This lack of knowledge of the multivariate structure of functional traits at intraspecific level is particularly embarrassing. Indeed, there has been wide recognition in the field of evolutionary quantitative genetics that the variability of single traits as well as the correlations between them at the population level can be key in driving local adaptation, shaping the boundaries of species' niches and determining their evolutionary potential (Kirkpatrick & Barton 1997; Gomulkiewicz & Houle 2009; Lavergne *et al*. 2010).

In this paper, we use the term 'functional variability' (hereafter FV) to jointly refer to the amount of variance in multiple functionally related traits (i.e. single-trait variances) and to the pattern of covariation between these traits, this later characteristic being known as 'phenotypic integration' (Pigliucci 2003). The functional variability of a population can be summarized by its phenotypic variance-covariance matrix and visualized as an ellipsoid in a multidimensional trait space (Fig. 1). This ellipsoid has three main features: (i) the extent of functional variability (hereafter FV extent), which represents the overall amount of phenotypic variability, is the volume of the ellipsoid; (ii) the shape of functional variability (hereafter FV shape), measured as whether the ellipsoid is closer to a sphere or to a segment, which describes the strength of the correlations between the different traits (i.e. the intensity of phenotypic integration) and (iii) the direction of functional variability (hereafter FV direction), which represents the main direction of variation in the multi-trait phenotypic space, is the main direction of the ellipsoid.

Based on this methodology, studying the link between multi-trait intraspecific FV and the ecological niche can be broken down into three main questions.

First, concerning FV extent, it is crucial to understand how it varies within the niche from its core to its edge. Several hypotheses exist regarding the mechanisms driving FV extent. On the one hand, stressful abiotic environments should reduce intraspecific FV due to strong directional selective pressures resulting in the environmental filtering of adapted phenotypes (Keddy 1992; see Arnold *et al*. 2008 for the effect of selection on genetic variability). This kind of strong environmental filtering is frequently observed at the interspecific level in extremely arid or cold environments where functional diversity at the community level is reduced (Cowling *et al*. 1994; de Bello, Leps & Sebastia 2006). On the other hand, strong biotic interactions in species-rich communities could result in larger intraspecific FV. Indeed, in such diverse communities, many different kinds of competitors with varying ecological strategies and different functional traits are likely to be encountered by different individuals of a same species. This should drive divergent selection and character displacement in different directions for different individuals in order to reduce competition for resources with individuals from other species (Brown & Wilson 1956), thus resulting in a wider spectrum of functional strategies in the local population (Reich *et al*. 2003). In any case, the effect of biotic interactions should be more important for traits that are related to coexistence mechanisms than for traits involved in the tolerance to abiotic conditions.

Secondly, it is important to understand what are the drivers of FV shape, and in particular in which part of the environmental niche the most integrated phenotypes are found. Theory predicts that correlational selection should be the main driver of strongly integrated phenotypes (Arnold *et al*. 2008), even though other genetic mechanisms could also increase trait correlations (Armbruster & Schwaegerle 1996). At the intraspecific level, phenotypic integration in plants has mainly been studied on floral morphology, with the recognition that strong selective pressures imposed by pollinators are responsible for the high degree of integration in floral structures (Berg 1960; Ordano *et al*. 2008; Armbruster *et al*. 2009). Concerning vegetative traits, it has been observed that plant species living in harsh environments often exhibit suites of functional traits that are strongly correlated (Chapin, Autumn & Pugnaire 1993). Several experimental studies have supported this view at the intraspecific level. For example, Gianoli (2004) showed that traits related to resource acquisition and growth in *Convolvulus arvensis* are more tightly correlated when environmental stress increases, which might be due to stronger energetic trade-offs between

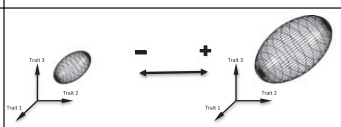
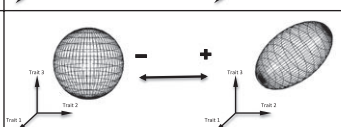
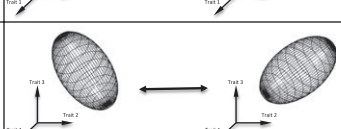
FV's characteristic	Description	Graphical representation	Statistical measure
Extent	Multi-trait functional variability		trace (***P***)
Shape	Strength of functional correlations		var(spectrum(***P′***))
Direction	Main direction of variation in multivariate space		$\boldsymbol{P}_{max}$: 1st eigenvector of ***P***

Fig. 1. Graphical representation of the functional variability of a population as an ellipsoid. Each of the three characteristics of FV translates into different kinds of ellipsoids, as exemplified by the pictures. Statistical measures of each characteristic are presented. P is the variance-covariance matrix of the selected traits. P′ is their correlation matrix.

several physiological functions (see also Schlichting 1989). According to these observations, we would expect that the most integrated populations be found at the niche edges, and particularly where abiotic conditions are limiting. However, Tonsor & Scheiner (2007) have found an opposite result in *Arabidopsis thaliana,* where the overall degree of phenotypic integration does not change with CO_2 availability.

Thirdly, examining FV direction provides interesting insights into the main drivers of functional trade-offs and the main axes of multivariate phenotypic variation at the population level. On the one hand, environmental factors could impose certain energetic constraints and thus settle trade-offs between several traits, resulting in natural selection shaping the main direction of phenotypic variation (Schluter 1996; Webb *et al*. 2010). This has been exemplified at interspecific level by the leaf economics spectrum, a single axis of variation that captures most of the variance in key foliar traits over thousands of plants from all around the world (Wright *et al*. 2004). However, if selection is the main driver of FV direction, there are no reasons why two populations that face different environments could not have different main axes of phenotypic variation. On the other hand, genetic factors like pleiotropic effects, random drift, asymmetric gene flow between source and sink populations or linkage disequilibrium between traits can increase correlations between certain pairs of traits and thus set the main directions of FV (Armbruster & Schwaegerle 1996; Gomulkiewicz & Houle 2009). In the case of extremely strong genetic control on FV direction, these directions should be the same among populations and within different populations (Sokal 1978; Armbruster & Schwaegerle 1996).

In this paper, we examine how these three different aspects of FV vary across the environmental niche of the widely distributed arctico-alpine plant species *Polygonum viviparum* L. Using robust statistical techniques borrowed from quantitative genetics, we studied the multivariate functional variability of different populations in natural conditions along an environmental gradient typical of alpine landscapes (i.e. temperature). We specifically ask the following questions:

1. How does the extent of intraspecific FV vary across spatial scales, that is, what is the importance of intrapopulation trait variability compared to interpopulation trait variability?
2. Does the extent of intraspecific FV increase from the warm to the cold edge of the species' niche due to the shift from environments dominated by competition to environments dominated by environmental filtering?
3. Is phenotypic integration higher at the edges of the niche due to more stressful conditions that impose stronger energetic trade-offs?
4. Do different populations share the same FV direction? And how does these directions relate to the environmental gradients and to the main direction of FV at the interpopulation level?

Material and methods

STUDY SPECIES AND SITE

We chose *Polygonum viviparum* L. as a model species because of its large environmental niche. This herbaceous perennial occurs in all arctico-alpine regions of the northern Hemisphere. In the Alps, it can be found from the montane belt (starting around 1000 m of altitude), where plant biomass is high and competition for light and nutrients severe, to the upper alpine level (ending at c.a. 3000 m a.s.l.), where the environment is harsher and physiological limitations are stronger (Körner 1999, see Appendix S2). It has a preference for relatively moist habitats. The species has the specificity of bearing both flowers and bulbils (clonal reproductive organs) on the flowering spike.

We studied the species in the central French Alps Guisane Valley (Fig. S1, Supporting information) where it occurs in a variety of ecological contexts (from forests dominated by *Larix decidua* Mill. to alpine screes). To maximize the environmental differences between sites (Albert *et al*. 2010c), we stratified the sampling design following two independent gradients known to have high impact on the physiology of alpine plants (Körner 1999): mean annual temperature and solar radiation in June. These two variables were selected from a set of climatic variables interpolated at 50-m resolution Aurelhy model, (Benichou & Le Breton 1987) extracted from all known occurrence points for *P. viviparum* in the Guisane valley (data collected by the National Botanical Alpine Conservatory, http://www.cbn-alpin.fr/). The selection was made by choosing two orthogonal gradients that strongly correlated with the two first axes of the principal component analysis conducted on this set of variables (results not shown).

Temperature was the main environmental gradient and the primary determinant for *P. viviparum*'s environmental niche in our study area (Thuiller *et al*. 2010; Boulangeat, Gravel & Thuiller 2012). This climatic variable acts on plant physiology and phenology, with colder sites being subject to more frequent frost events even during the summer and experiencing a shorter growing season. Temperature also plays an indirect biotic role in conjunction with soil by discriminating between warm productive species-rich habitats and cold unproductive species-poor habitats (Körner 1999). Using botanical surveys to estimate species richness per site as well as a spectral measure of overall biomass per area (NDVI, see Appendix S2), we confirmed that mean annual temperature was indeed positively correlated to both species richness ($R^2 = 0{\cdot}10$, $P = 6e{-}5$) and biomass per area ($R^2 = 0{\cdot}28$, $P = 0{\cdot}0005$).

This led us to interpret the temperature gradient as a climatic gradient influencing plant physiology and phenology but also as a gradient discriminating between sites mainly dominated by biotic vs. abiotic constraints. Such a contrast between the limiting role of abiotic stress at the cold end of the distribution and the primary importance of biotic interactions at the warm end of the distribution has recently been confirmed for several alpine plant species, including *P. viviparum* (Boulangeat, Gravel & Thuiller 2012). In contrast, even if it is usually an important gradient for alpine vegetation and although we explicitly sampled along it, solar radiation did not explain any FV characteristic at the population level: its influence is therefore not discussed in the following of this article.

FIELD TRAIT MEASUREMENTS

We sampled 29 populations at altitudes ranging from 1500 m to 2950 m, covering a large proportion of the climatic space occupied by the species in the study area [99% of the temperature gradient and 53% of the radiation gradient, Fig. S1 (Supporting information)]. Measurements were made at each population's

flowering peak in order to sample each population at the same phenological stage (July 2010). In each population (10×10 m), three subpopulations of 1×1 m were selected to represent contrasted microenvironmental conditions, using the same methodology as Albert *et al.*'s (2010b).

In each subpopulation, the following functional traits were measured on five randomly selected individuals: maximum vegetative height (H_{max}, top of plant photosynthetic tissue); total length of the inflorescence (H_{inflo}); ratio of sexual reproduction (SEX, ratio of the length of flowers divided by the total length of the spike); leaf dry matter content (LDMC, the ratio of leaf dry mass over fresh mass); specific leaf area (SLA, the ratio of leaf surface over fresh mass); leaf nitrogen content (LNC, the percentage of nitrogen in the dry mass of the leaf) and carbon-to-nitrogen ratio (C:N, the ratio of carbon over nitrogen in the leaf dry mass). These traits relate to various aspects of plant functional strategy (Westoby, Falster & Moles 2002), like resource acquisition and growth rate (LDMC, SLA, LNC, C:N), ability for light competition (H_{max}) and reproductive effort (H_{inflo} and SEX). Foliar traits are known to be physiologically correlated due to leaf economics constraints (Wright *et al.* 2004) and are thus suited to studying phenotypic integration. However, energetic trade-offs could also arise at the whole plant level due to resource allocation conflicts between growth, longevity and reproduction (Chapin, Autumn & Pugnaire 1993; Enquist *et al.* 1999; see Diggle 1997 for allocation in *P. viviparum*); our decision to include H_{max}, H_{inflo} and SEX was intended to include this higher-level trade-off.

CHARACTERIZING FUNCTIONAL VARIABILITY IN WILD POPULATIONS

Overall trait variability

To quantify the extent of intraspecific functional variability in the whole data set and understand the structure of intraspecific FV across spatial scales, we first broke down the variability of each trait at different hierarchical levels using mixed effects regression models. To do this, we used intercept models with random effects corresponding to the different levels of hierarchy (i.e. population and subpopulation nested in population). We then extracted the percentage of variance explained by each hierarchical level for each trait. Variance components were estimated using restricted maximum likelihood (REML).

To get a finer understanding of trait variation across our study area, we also examined the response of all traits against the temperature gradient, using linear or quadratic models with the same random effects as mentioned previously to account for the hierarchical structure of the data set. *P*-values for such models were obtained by likelihood ratio tests, using an R function provided by Christopher Moore (http://blog.lib.umn.edu/moor0554/canoemoore/2010/09/lmer_p-values_lrt.html).

To quantify FV extent for each population, all traits were transformed to have a mean of zero and a standard deviation of one across the whole sample. Thus, all traits have equal importance in the subsequent analyses. For each population, a variance-covariance matrix for the seven traits was built (**P**-matrices). Overall trait variability (i.e. FV extent) in a population was measured as the trace of **P** (i.e. the sum of its diagonal elements), a measure commonly used for genetic variance matrices (Revell 2007).

Phenotypic integration: patterns and causes

A matrix of correlations between the seven traits was built for each population (**P′**-matrices), and the variance of the eigenvalues of **P′** was taken as an index of integration (i.e. FV shape, Cheverud, Wagner & Dow 1989), higher values meaning stronger correlations between traits.

The direction of phenotypic integration was compared between populations by determining the axis of maximum phenotypic variation, P_{max} (first eigenvector of **P**, also known as 'the line of least resistance', Schluter 1996), for each population. For each couple of populations, one minus the correlation between their P_{max} was used to measure the functional distance between them, producing a matrix of functional distances between populations (**P-dist**).

To test whether and how environmental or genetic constraints drive FV direction, we compared **P-dist** to different environmental distance matrices (Euclidean distance on the climatic plane defined by temperature and radiation and Euclidean distance on the temperature gradient only) and geographical distances using Mantel tests. As the influence of gene flow between populations was expected to mainly play a role at small geographical scales (of the same order of magnitude as the species' dispersal distance), we also used Mantel correlograms to unravel these small-scale dependencies.

We conducted the same analysis on FV direction using Random Skewers (Cheverud 1996) to measure functional distances between populations. Although Random Skewers were originally designed to compare the responses of different populations to putative selection events, they can also be used to compare all kinds of variance-covariance matrices (e.g. Kolbe *et al.* 2011) and have advantages over P_{max} methods in that they compare the properties of entire matrices. This additional procedure was used to back up the results obtained with the P_{max} analysis and led to the same conclusions (detailed method, R code and results for Random Skewers are available in Appendix S3).

ROBUSTNESS OF MATRIX ESTIMATION

Given our sampling implied a low number of measured individuals within each population (i.e. 15), it could impede robust estimation of the **P** and **P′** of each population. We measured the robustness of matrix estimation using a bootstrapping procedure (Cheverud, Wagner & Dow 1989) and found that on average there are 7·1% of chances that differences between two **P** matrices are not meaningful and 14·3% of chances for **P′** matrices (detailed description in Appendix S5). This uncertainty is however counterbalanced by the two main strengths of our approach which are that (i) we studied FV within and among numerous (i.e. 29) populations of the same species, thereby rendering our analyses less sensible to this matrix estimation error, and (ii) followed a stratified hierarchical sampling along *in situ* and continuous environmental gradients. This should provide a more comprehensive picture of trait variability and integration across the whole niche of the study species than what is generally done under controlled conditions on few discrete environmental conditions.

Results

EXTENT OF TRAIT VARIABILITY

Variance decomposition revealed two different cases. In the case of vegetative height (H_{max}), most of the variation (73%) was found between populations. Conversely, for all other traits included in our study, around half of the variance occurred between individuals of the same subpopulation (Table 1). Overall, there was little variation between different subpopulations (1–21% depending on the trait). The subsequent analyses carried out at population level were then justified, as FV was rather high within populations.

All of the traits we studied except SEX showed a significant relationship with mean annual temperature (see

Table 1. Variance decomposition of the different traits. The percentage of variance explained by the different hierarchical levels is shown for each of the seven functional traits. Coefficients of variation are presented in the last row

Hierarchical level/Trait	H_{max}	SEX	H_{inflo}	LDMC	SLA	C:N	LNC
Population	73	17	46	42	56	38	42
Subpopulation	6	21	8	6	10	1	3
Individuals	21	62	46	51	34	61	55
Coefficient of variation	0·43	1·52	0·34	0·14	0·28	0·26	0·24

Fig. 2). Mean population values of LDMC and LNC decreased with temperature, while SLA, C:N and H_{inflo} increased with temperature. H_{max} showed a quadratic relationship, reaching a maximum value for intermediate temperatures.

FV extent (overall trait variability) in each population positively correlated with the mean annual temperature of the site (R^2 = 18%, P = 0·012, see Fig. 3). No significant relationship was found with solar radiation.

PHENOTYPIC INTEGRATION

The strength of phenotypic integration was in general relatively high for all populations. Indeed, under the assumption of no correlation between the seven traits studied and given that we sampled 15 individuals per population, the expected value for the integration index is 0·4 (Wagner 1984). To evaluate a confidence interval for that value, we built a null distribution for the integration index by randomly sampling seven trait values for 15 individuals (Gaussian traits, 100 000 resamples) and computing the integration index. We obtained a 95% quantile of 0·75. Observed values of phenotypic integration across the 29 populations were always significantly stronger than randomly expected (min = 0·77) and were on average rather high (mean = 1·23).

This integration showed a triangular relationship with mean annual temperature (Fig. 3). This result was not dependent on the traits included in **P** (results not shown). Quantile regressions confirmed that the most integrated populations were found at the middle of the temperature gradient, which corresponds to the niche core: the 75% percentile of the distribution of integration values shows a quadratic relationship with temperature (P-value = 0·022).

The main directions of phenotypic integration, estimated by P_{max}, generally correlated between populations (cor = 0·48 ± 28). No general line of least resistance emerged although most of the P_{max} were directed towards high variance in LNC. Interestingly, the main direction of phenotypic variation for all 29 populations pooled together is orthogonal to this dominant intrapopulation direction (results from a PCA, see Fig. 4).

The differences in the main directions of phenotypic integration between populations were not explained by environmental nor geographical distance, as all the Mantel tests were non-significant (P-values = 0·328; 0·793 and 0·668 for environmental, temperature and geographical distances, respectively). However, FV direction in

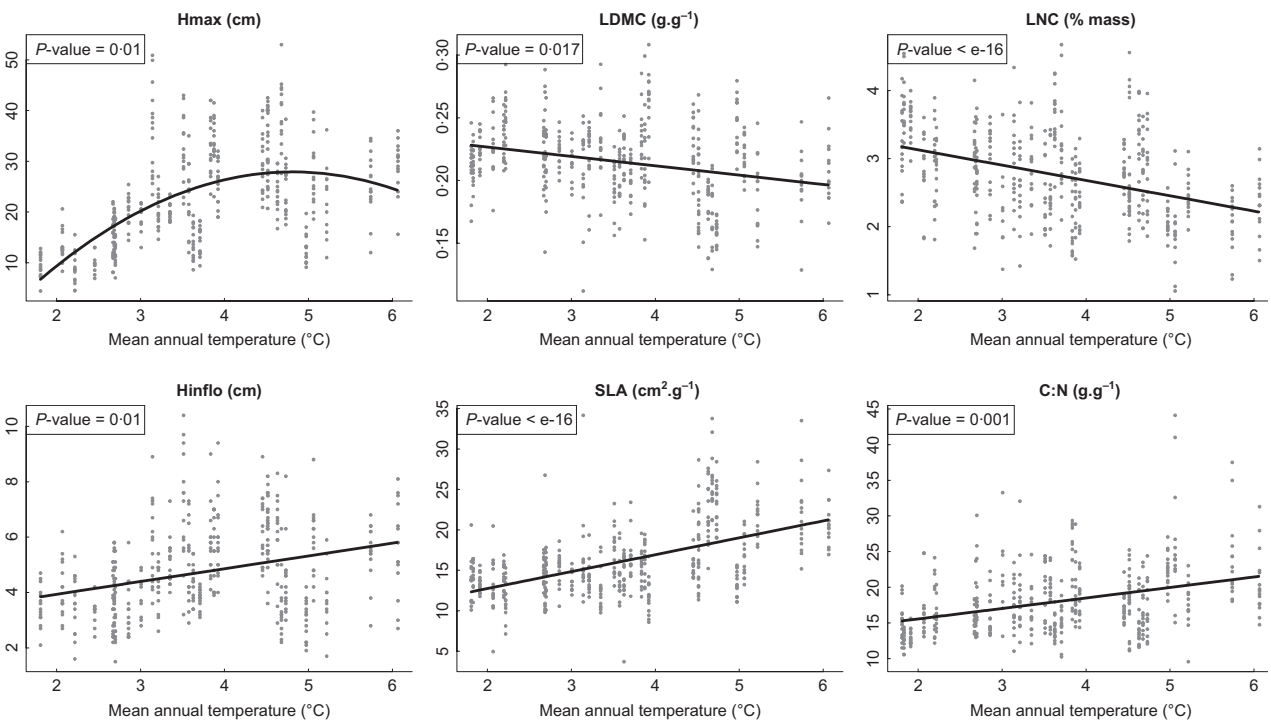


Fig. 2. Response of functional traits to the temperature gradient. Individual trait measures for all traits except SEX are plotted in grey. Black lines show the regression lines (quadratic regression in the case of H_{max}).

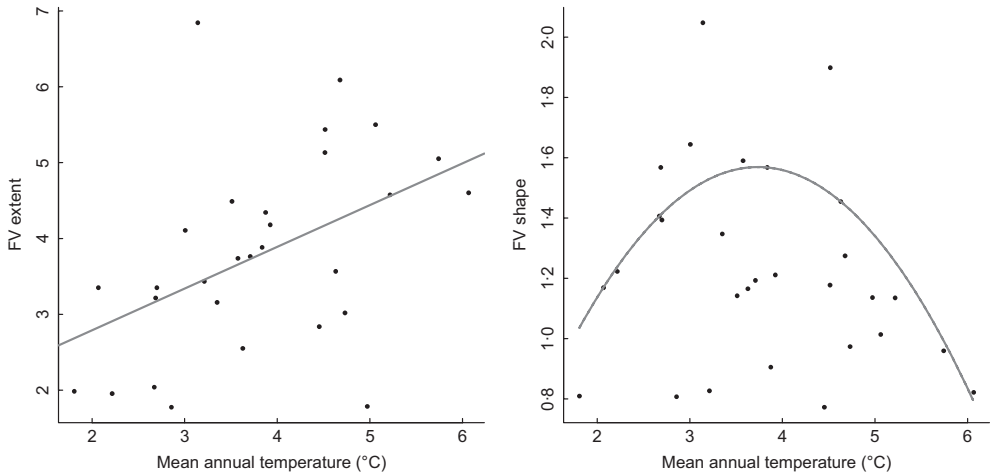


Fig. 3. *Left panel*: Relation between overall trait variability (FV extent) and mean annual temperature. Black dots represent each of the 29 populations sampled. The regression line is drawn in grey ($P = 0{\cdot}012$). Overall trait variability increases with temperature. To get an idea of the unit, the extent of FV across the 29 populations equals 7. *Right panel*: Relationship between the strength of phenotypic integration (FV shape) and mean annual temperature. The parable represents the quadratic regression for the 75% percentile ($P = 0{\cdot}022$). The most strongly integrated populations are found on the middle of the gradient. All values are above 0·75 and thus represent significant integration.

populations tended to be positively correlated at short distances [<200 m, cor = 0·083, $P = 0{\cdot}043$, Fig. S4 (Supporting information)], but no relation between functional and geographical distances was found for larger distances.

Discussion

Our study reveals some general patterns of functional variability in *P. viviparum*. The primary observation is that trait values are highly variable and that a large proportion of this variation is found between individuals of the same population, confirming previous observations on plants (Albert *et al*. 2010b; Messier, McGill & Lechowicz 2010). This could be due to high levels of phenotypic plasticity, but the fact that our attempt to distinguish subpopulations does not explain much FV may also reveal that microenvironmental heterogeneity plays a role at a smaller scale than the one we chose (1 1 m), possibly at individual scale. This highlights the importance of studying FV within populations. However, populations do exhibit some differences, and temperature strongly influences mean trait values at the population level, as already observed for various types of alpine plants including *P. viviparum* (Albert *et al*. 2010b). High values of LDMC and LNC along with

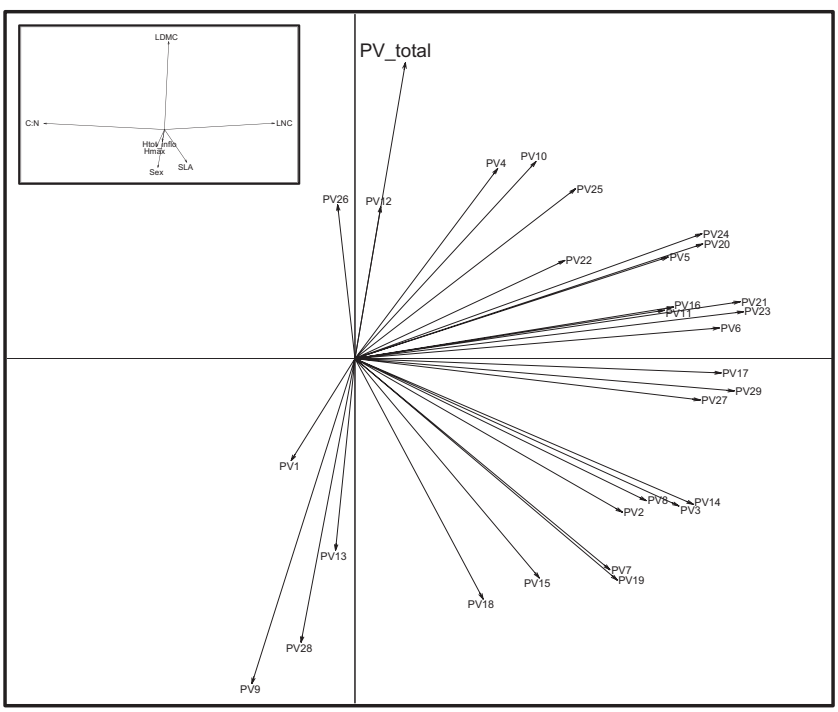


Fig. 4. Results of a PCA on the P_{max} of the 29 populations studied as well as the general P_{max} for all populations combined (PV_total). The 'line of least phenotypic resistance' for each population is projected on the plane defined by the two first PCA axes. The *top-left* plot shows the different trait variances in relation to the PCA axes. Note that most of the P_{max} for populations are directed towards high variance in LNC and low variance in C:N, while the general P_{max} is orthogonal to most of them and directed towards high variance in LDMC.

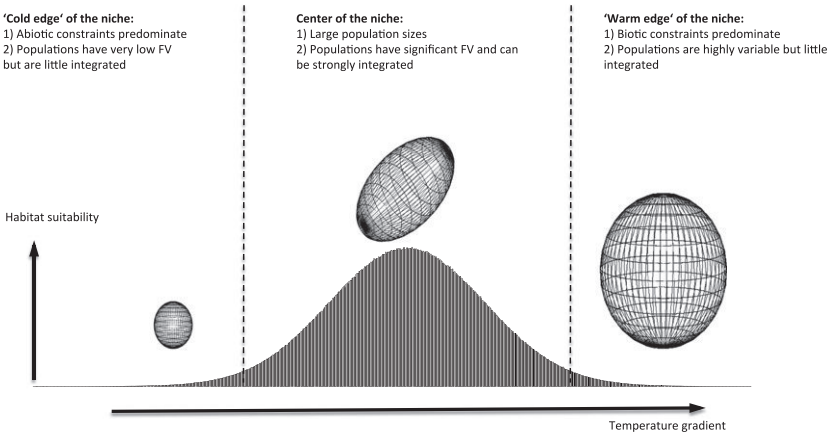


Fig. 5. FV structure in populations located in different parts the environmental niche. This illustration is meant to summarize the main findings of our study, and differences between populations have been exaggerated for clarity. The environmental niche of *P. viviparum* can be symbolically represented along the temperature gradient, the grey Gaussian curve representing values of habitat suitability. The niche has been cut into three main parts for simplicity, according to the results: the niche centre and the 'cold' and 'warm' edges. The size and shape of the ellipsoids represent, respectively, FV extent and shape: smaller volumes meaning low FV and volumes close to spheres representing less integrated populations.

low values of H_{max} and SLA for populations at the cold end of the gradient are characteristic of stressful environments (Chapin, Autumn & Pugnaire 1993) and indicate cold tolerance in these populations (Reich *et al.* 2003).

When trying to understand how FV extent is structured across *P. viviparum*'s niche, we found that the overall trait variability increases with mean temperature. This pattern supports the hypothesis that habitat filtering prevails in environments dominated by abiotic constraints (cold edge of the niche) and that functional divergence may be high within communities with a high number of interspecific biotic interactions (warm edge of the niche). Such a pattern of increased trait variability in richer communities has already been observed for morphological traits in grasshoppers of the genus *Melanoplus* (Roff & Mousseau 2005). In the case of *P. viviparum*, the very harsh conditions experienced in alpine habitats should lead to strong directional selection pressures for increased resistance to cold, drought and high solar radiation, whereas in the warmer subalpine meadows plant competition is expected to be stronger and lead to phenotypic divergence for niche partitioning between interacting individuals, thus resulting in increased trait variance within species (Weiher & Keddy 1995; Cornwell, Schwilk & Ackerly 2006; but see Spasojevic & Suding 2011).

We also observed that phenotypic integration is in general relatively high within *P. viviparum* populations. This is primarily due to the strong correlations between the four foliar traits included in this study (cor = 0·45 ± 0·32 in absolute value over the 29 populations), which are known to reflect the world-wide leaf economics spectrum (Wright *et al.* 2004). The allometric correlation between H_{max} and H_{inflo} explains the rest of this pattern. Yet, no systematic trade-off was detected between reproductive, growth and persistence functions (the mean correlation for H_{inflo} with any of the foliar traits is always <0·08 in absolute value). Note that the allocation to sexual reproduction (SEX) is a very idiosyncratic trait that does not correlate to the environmental gradients in our study area (contrary to what has been observed in the Arctic by Dormann, Albon & Woodin 2002), nor to any other trait measured.

One important finding is that the most integrated populations are found at the centre of the niche (i.e. middle of the temperature gradient, see Fig. 3). This result is contrary to our expectations and contrasts with some studies in controlled conditions where phenotypic integration has been found to increase with stress (e.g. Schlichting 1989; Gianoli 2004). We suggest that this pattern could be due to demographic asymmetries between the centre and the margins of the niche. Indeed, many theoretical models suggest that the larger population sizes at the centre of the niche lead to a better response to natural selection (e.g. Kirkpatrick & Barton 1997), which could produce integrated, more 'optimized' phenotypes. Conversely, marginal populations could be subject to high levels of both genetic drift and gene flow from the central populations, rendering selection inefficient and leading to low integration (Sexton *et al.* 2009). In our study area, we verified that population size is on average higher in the middle of the temperature gradient (F. Boucher, field observation).

The last attribute of FV that we intended to study was its direction. We found that the main axis of trait variation within populations is often related to variance in leaf nitrogen content, a trait linked to soil nitrogen uptake efficiency in fertile environments (Zatylny & St-Pierre 2006) and which also strongly affects the plant's photosynthetic rate (Reich, Walters & Ellsworth 1991). This high variation in LNC within populations might be explained by the heterogeneity of the nitrogen supply in soils. This heterogeneity is both qualitative and quantitative: nitrogen can be present either in its organic form, which is costly to acquire, or in the form of ammonia or nitrates, and the amount of

these alternative forms varies spatially. Indeed, it has been revealed that fine-scale factors like soil characteristics have a great influence on the functional diversity of plant communities in the Guisane valley (Bello *et al*. in press). The slightly lower variances in LNC and C:N found in colder populations of *P. viviparum* could be due to the predominance of organic nitrogen in high altitude sites (Averill & Finzi 2011) or to less spatial heterogeneity in soil nitrogen concentrations in these habitats, relative to subalpine ones. Interestingly, the main direction of phenotypic variation at the interpopulation level is almost orthogonal to this general intrapopulation direction and lines up with traits that are more directly related to the abiotic environment, supporting the main axis of variation observed at the interspecific level in plants. Indeed, H_{max} strongly correlates with temperature in our study area (Fig. 2), ranging from more than 50 cm in subalpine meadows to less than 5 cm in the alpine sites. LDMC is also strongly affected by climatic conditions because it is expected to increase leaf longevity and thus resource conservation, which are likely to be favoured in stressful habitats. This suggests that the main functional trade-offs revealed for plants at the interspecific level (e.g. leaf economics spectrum) over large geographical gradients might not be reflected at finer spatial scales (e.g. population level). This finding could have profound implications for the study of local coexistence in community ecology. A similar result has already been found for two forest herb species that show an opposite pattern of correlation between plant height and seed mass at the intraspecific level than the one observed at the interspecific level (De Frenne *et al*. 2011). The fact that environmental distances do not correlate with functional distances between populations (measured either by P_{max} or by Random Skewers correlations) confirms that climate is not the main driver of FV direction at the population level. On the contrary, the strong spatial autocorrelation that we found at small distances in the functional structure of populations suggests that high genetic similarity between close populations could result in very similar integration patterns (Stone, Nee & Felsenstein 2011). However, the fact that the main direction of integration differs significantly between populations shows that genetic correlations between traits are not excessively strong (Armbruster & Schwaegerle 1996).

Given that additive genetic variances were not measured and that the level of heritability for each studied trait is uncertain (Ackerly *et al*. 2000; Geber & Griffen 2003), any potential evolutionary interpretations of the patterns we report must be cautious. It is indeed possible that differences in intraspecific FV structure are only due to differences in genetic diversity in our populations arising from past demographic fluctuations (Wright 1969). However, these differences might as well be largely due to phenotypic plasticity (Pigliucci 2003) and in particular to the fact that individuals living in high-resource environments are expected to be more plastic than their stressed conspecifics (Chapin, Autumn & Pugnaire 1993; Grassein, Till-Bottraud & Lavorel 2010). Integrating direct measurements of genetic diversity and the relatedness of populations in the kind of ecological study proposed herein might constitute a promising avenue for future research (e.g. Martin, Chapuis & Goudet 2008) and will help to disentangle the relative effects of ecology, demography and genetics on the functional variability of populations.

Conclusion

Put together, our results give a clearer picture of how intraspecific FV is structured in different parts of *P. viviparum's* environmental niche (Fig. 5). Indeed, populations at the 'cold end' of the niche have low FV but are mildly integrated. Populations located at the centre of the niche have intermediate trait variability and varying degrees of integration, but some are subject to strong trade-offs between traits. Finally, populations of the 'warm end' of the niche are both highly variable and little integrated. Our study thus shows the importance of the environment in setting FV extent and reveal substantial asymmetry in the species' environmental niche between its 'biotic' and 'abiotic' edges. Interestingly enough, this finding corroborates hypotheses and observations traditionally made in community ecology that strong abiotic filters lead to greater functional convergence between species coexisting within natural communities (Webb *et al*. 2002). Finally, we demonstrate that the main functional trade-offs differ within and among populations and that the idea that phenotypic integration increases in stressful environments cannot be considered a rule.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. 3D map of the Guisane valley, stretching from Briançon (1200 m a.s.l.) to the Pic Blanc du Galibier (2955 m a.s.l.) in the inner French Alps. The Lautaret pass is located at 2050 m and the Guisane river is drawn in white. The 29 sampled populations of *P. viviparum* are shown in black dots. The map is colored according to the mean annual temperature (from white to black when going to colder sites, source: Aurelhy model [Benichou & Le Breton 1987)]. The small plot in the bottom-left corner shows the position of the sampled populations (black dots) and of all populations of *P. viviparum* of the Guisane Valley recorded by botanists of the CBNA (grey dots) in the climatic plan defined by mean annual temperature and solar radiation in June. The temperature gradient is particularly well covered (99%).
Fig. S2. Plot of NDVI vs. mean annual temperature for 36 populations (including the 29 presented in this study) of *P. viviparum* in the Guisane Valley. The regression line is drawn in red.
Fig. S3. Relation between plant species richness and mean annual temperature in the Guisane valley.
Fig. S4. Correlograms for **P-dist** (left) and **RS-dist** (right), black squares meaning that the values of correlations are significantly different from zero and the first point corresponding to all pairs of populations that are closer than 200 m.
Fig. S5. Results of a PCA lead on all 'lines of least resistance': general metapopulation value (PV_total, circled in red), observed population values and bootstrapped values (2930 vectors). P_{max} are plotted on the two first axes of the PCA. The bottom-left panel shows how the seven traits relate to these axes.
Table S1. *P*-values of the Mantel tests.
Table S2. *P*-values of the partial mantel tests between functional distances and environmental distances, where geographic distance between populations was used as a covariate.

Résumé

La niche climatique des espèces joue un rôle important dans la distribution spatiale de la biodiversité, mais la manière dont les niches climatiques évoluent reste encore peu connue. Ce travail vise à révéler la manière dont les niches climatiques évoluent en général, et plus précisément à déterminer comment certaines plantes se sont adaptées aux environnements alpins. En étudiant de nombreux groupes de plantes, de poissons, de mammifères et d'oiseaux, nous avons montré que les niches climatiques évoluent le plus souvent par à-coups et non pas de manière graduelle. Elles restent en effet stables pendant des périodes de plusieurs millions d'années puis évoluent de manière extrêmement rapide avant de se stabiliser à nouveau dans une autre gamme de climat. Des simulations ont permis de montrer que les phases de relative stabilité n'étaient pas forcément causées par une sélection stabilisante sur les niches climatiques mais pouvaient également résulter de la présence de barrières géographiques qui empêchent les espèces d'expérimenter de nouveaux climats. L'étude de l'histoire des plantes du genre *Androsace* a révélé que les changements rapides de niches correspondaient au contraire à l'apparition de nouveaux traits, comme la forme de vie en coussin. Ce travail montre que de nombreux facteurs influencent l'évolution des niches climatiques et souligne la nécessité de tous les étudier ensemble.

Summary

Species' climatic niches play an important role in the spatial distribution of biodiversity but the way climatic niches evolve remains poorly known. This works aims at determining the general mode of evolution of climatic niches, and more precisely at revealing how some plants have adapted to alpine environments. The study of many groups of plants, fishes, mammals and birds has shown that climatic niches usually evolve by fits and starts but not gradually. Niches indeed remain stable over million years before evoving extremely quickly and stabilizing again in a new range of climates. Simulations have shown that these phases of relative stability need not be caused by stabilizing selection but can also be caused by geographic barriers that prevent species from experiencing new climates. The study of the history of plants of the genus *Androsace* has revealed that rapid niche shifts on the contrary resulted from the appearing of novel traits, like the cushion life form. This work shows that numerous factors contribute to the evolution of climatic niches and emphasizes the necessity to study them together.